Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA

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ABSTRACT

Symmetrodont mammals, generally rare and poorly represented in the fossil record, are exceptionally abundant in the Mussentuchit local fauna of the upper Cedar Mountain Formation (upper Albian or lower Cenomanian), Emery County, Utah, USA. Herein we describe three new species of symmetrodonts (four or more are present in the fauna); one is referable to *Spalacotheridium*, otherwise known from the Turonian (Late Cretaceous), and the other two are referred to a new genus. With the possible exception of *Mictodon*, all North American Cretaceous symmetrodonts are referable to the Spalacotheriidae. Spalacotheriids are distinctly different from more primitive symmetrodonts such as *Kuehneotherium* in jaw structure (e.g., detachment of postdentary elements, presence of pterygoid crest) and molar morphology and function (e.g., development of continuous mesial and distal shearing surfaces). To this extent, they are more clearly similar to tribosphenic therians than are archaic symmetrodonts, although they are uniquely specialized. Some features of advanced spalacotheres, such as the loss of the coronoid and meckelian groove, developed convergently in tribosphenidans and many other groups, and hence represent iterative themes in the evolution of Mesozoic mammals. Features of the molars and dentary suggest that the Family Spalacotheriidae is a monophyletic group, with the European *Spalacotherium* and Chinese *Zhangheotherium* forming successive outgroups to remaining genera. Within the family, North American taxa appear to form a monophyletic clade, culminating in the highly specialized *Symmetrodontoides* of the Late Cretaceous; *Microderson*, known only by a single upper molar from the Cretaceous of Morocco, is of enigmatic affinities. Spalacotheriids were clearly present in North America by the Aptian-

KEY WORDS
Symmetrodonta,
Spalacotheriidae,
phylogeny,
Cretaceous.

Albian and, assuming that North American taxa form an endemic and exclusive monophyletic group, their presence on the continent cannot be attributed to an hypothesized mid-Cretaceous interchange with Asia. Instead, phylogenetic data suggest their origin from western Europe sometime in the Early Cretaceous, supporting the hypothesis that there was some degree of faunal continuity at that time between the two landmasses, based initially on similarities of the dinosaur assemblages.

RÉSUMÉ

Les symmétrodontes spalacotheriidés (Mammalia) du Crétacé (Albien supérieur ou Cénomanien inférieur) de la faune de Mussentuchit, Formation Cedar Mountain, Utah, USA.

Les mammifères symmétrodontes, qui sont généralement rares et mal représentés dans le registre fossile, sont exceptionellement abondants dans la faune locale de Mussentuchit du sommet de la Formation « Cedar Mountain » (Albien supérieur ou Cenomanien inférieur), Emery County, Utah, USA. Nous décrivons ici trois nouvelles espèces de symmétrodontes (il existe au moins quatre espèces dans la faune de Mussentuchit) ; une espèce se rapporte au genre *Spalacotheridium*, connu par ailleurs dans le Turonien (Crétacé supérieur), et les deux autres sont attribuées à un nouveau genre. À l'exception, peut-être, de *Mictodon*, tous les symmétrodontes nordaméricains appartiennent à la famille des Spalacotheriidae. Ces derniers diffèrent nettement des symmétrodontes plus primitifs tels que *Kuehneotherium* par la structure de leur mâchoires (entre autres, le détachement des éléments postdentaires et la présence d'une crête ptérygoïde) et par la morphologie et la fonction de leurs molaires (entre autres, le développement de surfaces coupantes continues mésiales et distales). Sur ce plan, ils ressemblent plus à des thériens tribosphéniques qu'à des symmétrodontes archaïques, bien que présentant des spécialisations uniques. Quelques caractères de spalacothères dérivés, tels que la perte du processus coronoïde et du sillon de meckel se développent de façon convergente chez les *Tribosphenida* et de nombreux autres groupes, et constituent des thèmes répétitifs dans l'évolution des mammifères mésozoïques. Les caractères des molaires et du dentaire suggèrent que la famille des Spalacotheriidae constitue un groupe monophylétique, le genre européen *Spalacotherium* et le genre chinois *Zhangheotherium* formant les extra-groupes successifs des autres genres. Au sein de la famille, les taxons nordaméricains semblent constituer un clade monophylétique qui culmine avec les formes hautement spécialisées comme *Symmetrodontoides* du Crétacé supérieur ; les affinités de *Microderson*, connu par un seule molaire supérieure du Crétacé du Maroc, restent énigmatiques. Les spalacotheridés étaient clairement présent en Amérique du Nord dès l'Albien-Aptien et, si l'on admet que les taxons nord-américains constituent un groupe monophylétique endémique et exclusif, leur présence sur le continent ne peut être attribuée à un éventuel échange faunique avec l'Asie au milieu du Crétacé. En revanche, les données phylogénétiques suggèrent que l'origine des Spalacotheriidae se situe en Europe occidentale au Crétacé inférieur, renforçant ainsi l'hypothèse selon laquelle il existait, à cette époque, une certaine continuité faunique entre les deux continents, hypothèse fondée initialement sur les ressemblances observées entre les faunes de dinosaures.

MOTS CLÉS
Symmetrodonta,
Spalacotheriidae,
phylogénie,
Crétacé.

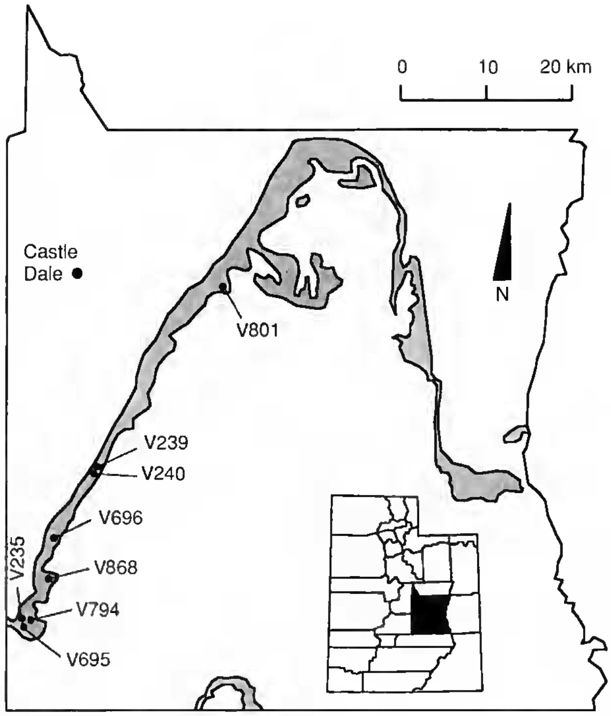

FIG. 1. — Outcrop map of the Cedar Mountain Formation, Utah (inset), and field area in Emery County. Localities are OMNH sites that produced specimens of Spalacotheriidae described in the text (see Cifelli *et al.* 1999, for sections showing stratigraphic positions of sites).

INTRODUCTION

Symmetrodonts have long been accorded a critical position in mammalian evolution because the principal cusps of upper and lower molars form the "reversed triangle" pattern that is widely believed to be morphologically intermediate between the serially tricuspid condition of triconodonts and the more elaborate molars of tribosphenic mammals (e.g., Patterson 1956). Unfortunately, their fossil record is abysmal, and they are probably the worst represented of all Mesozoic mammal "groups" (in a morphological, not taxonomic sense) – the recent discovery of an exceptional specimen from the Late Jurassic or Early Cretaceous of China (Hu *et al.* 1997, 1998) notwithstanding. Given the fact that knowledge of symmetrodont diversity and morphology is poor, it is unsurprising that they are generally omitted from comprehensive analyses of mammalian phylogeny (e.g., Rowe 1988; Wible 1991; Wible & Hopson 1993; Rougier *et al.* 1996), notable exceptions being the works of Prothero (1981) and Hu *et al.* (1997). In North America, symmetrodonts were long known from the Late Jurassic only, as represented by *Tinodon* Marsh, 1879 and the probably synonymous *Eurylambda* Simpson, 1929 (see Simpson 1929; Crompton & Jenkins 1967; Prothero 1981). Later discoveries recorded the survival of apparent "acute-angled" spalacotheriids, hitherto represented only in what was then considered the Jurassic of England, in the Early Cretaceous of Texas (Patterson 1955, 1956) and the Late Cretaceous of Alberta (Fox 1972, 1976, 1985) and southern Utah (Cifelli & Madsen 1986; Cifelli 1990). *Mictodon* Fox, 1984, an apparently relictual taxon from the Campanian of western Canada, represents the only record of an "obtuse-angled" symmetrodont from the Cretaceous of North America (Fox 1984b).

Herein we describe new taxa of intermediate age between these Early and Late Cretaceous records in North America. One of the taxa, at least, is represented by an unusually comprehensive series, affording the opportunity to examine variation and positional changes in the molar series, and presenting new information on the dentary of advanced Spalacotheriidae. Finally, we briefly comment on the status and placement of the Spalacotheriidae with respect to other symmetrodonts and to more advanced mammal groups, and provide an hypothesis of relationships within Spalacotheriidae.

The symmetrodonts described herein were collected from the Cedar Mountain Formation, Emery County, Utah. This unit was named for a series of terrigenous sedimentary rocks lying between the Upper Jurassic Morrison Formation and the Upper Cretaceous Dakota Formation (Stokes 1944, 1952), and is broadly exposed in central and eastern Utah (Fig. 1). Five units (in ascending order) of the formation are now recognized: the Buckhorn Conglomerate, and the Yellow Cat, Poison Strip Sandstone, Ruby Ranch, and Mussentuchit members (Kirkland *et al.* 1997). The symmetrodont specimens resulted from a concerted collecting effort in a restricted stratigraphic interval of the uppermost unit, the Mussentuchit Member, 10-20 m below the contact with the overlying Dakota Formation. The specimens described herein derive from eight sites (Fig. 1); the vast majority were collected from OMNH locality V695. The fossil horizon at this locality is directly overlain by a volcanic ash. Multiple, concordant ^{40}Ar/^{39}Ar determinations on sanidine phenocrysts from this ash, and from the same horizon nearby, yield a date of 98.39 ± 0.07 Ma (Cifelli *et al.* 1997); hence, the fauna is indistinguishable in age from the Albian-Cenomanian (Early-Late Cretaceous) boundary, placed at 98.5 ± 0.5 Ma by Obradovich (1993) and at 98.9 ± 0.6 Ma by Gradstein *et al.* (1995). Stratigraphic sections showing placement of the principal fossil localities are given in Cifelli *et al.* (in press).

The vertebrate assemblage from the upper part of the Cedar Mountain Formation, termed the Mussentuchit local fauna, is known by more than 5000 specimens representing about 80 taxa (Cifelli *et al.* 1999). Of the mammals, only the marsupial or near-marsupial *Kokopellia* Cifelli, 1993 (see Cifelli 1993; Cifelli & Muizon 1997), three triconodontids (Cifelli & Madsen 1998), and several multituberculates (Eaton & Nelson 1991) have been described thus far.

METHODS

Specimens were recovered using a combination of standard quarry procedures, through which most of the dentulous jaw fragments and a few of the larger isolated teeth were recovered, coupled with a large-scale underwater screenwashing operation (Cifelli *et al.* 1996; Madsen 1996). It is worthwhile pointing out that most of the isolated teeth were recovered from the fine fraction of internested screen boxes, in which the corresponding screen size was 30-mesh; had only window screen been employed, as is common practice for Late Cretaceous rocks of the US, few of these specimens (most of which have a maximum dimension of significantly less than 1 mm) would have been recovered.

Measurements were taken with a Reflex microscope, which permits non-contact recording of point coordinates in three dimensions; minimum standard errors are two microns on the x, y-axes and five microns on the z-axis (MacLarnon 1989). Reflex data are automatically recorded to 0.001 mm, and these data are reproduced verbatim here, although we point out that this does not take into account measurement error (see Lillegraven & Bieber 1986).

Measurements are shown in Figure 2. Spalacotheriid molars are extremely small and fragile; the lower molar cingula are particularly vulnerable to breakage. In order to maximize sample size for lower molars, we took standard length and width measurements minus the cingulum. We remeasured specimens of other relevant Spalacotheriidae using the same procedure; measurements of *Spalacotheroides bridwelli* Patterson, 1955 are from an epoxy cast, and those of *Symmetrodontoides canadensis* Fox, 1976 are from Fox (1976, fig. 5; 1985, fig. 1). Other measurements were taken by defining points at the apices of the primary cusps (paraconid, protoconid, metaconid) and calculating: (1) the distances between them; (2) the angle (herein called trigonid angle) formed between the points, with the protoconid at the apex. The trigonid angle is rather variable, even among teeth of the same locus. Consideration of tooth morphology suggests that the trigonid angle decreases with wear: the mesial and distal faces of the paraconid and

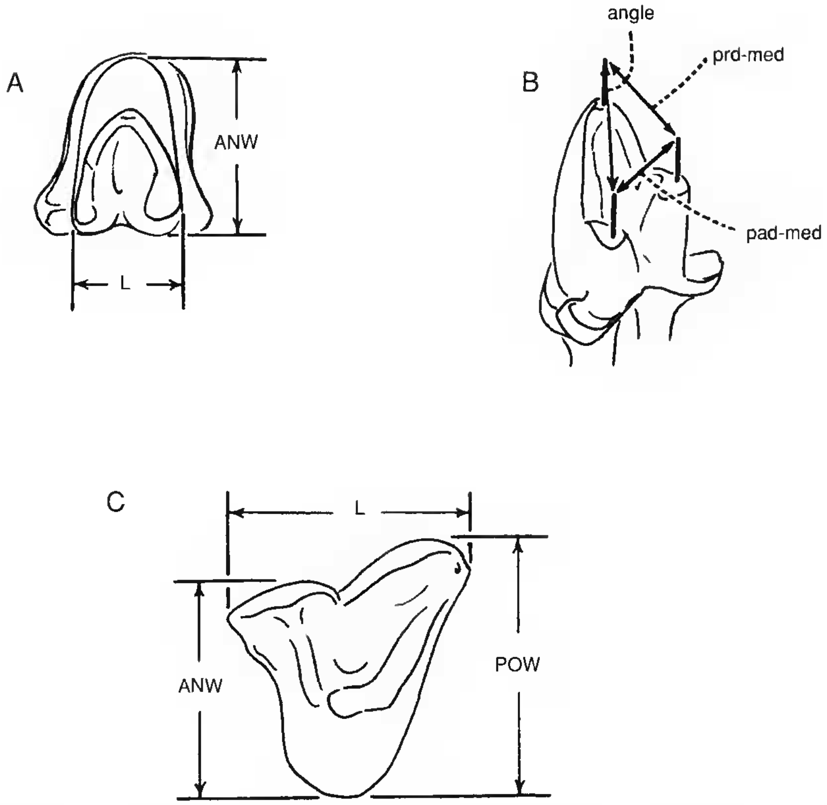

FIG. 2. — Spalacotheriid molars showing measurement conventions; **A**, right lower molar, occlusal view; **B**, right lower molar oblique occlusolingual view; **C**, left upper molar, occlusal view. Abbreviations: **angle**, angle formed by lines connecting apices of paraconid to protoconid and metaconid to protoconid; **ANW**, anterior width (greatest width of lower molars); **L**, mesodistal length; **pad-med**, distance from apex of paraconid to apex of metaconid; **POW**, posterior width; **prd-med**, distance from apex of protoconid to apex of metaconid.

metaconid (respectively) are rather vertical, whereas their opposing faces slope downward toward each other, so that the apparent centers of the cusps will migrate toward each other as wear progresses. We also attempted to take height measurements. However, our efforts were frustrated by our inability to define a repeatable plane of reference, and the fact that wear varies considerably from one specimen to the next. Hence, references to difference in crown height are qualitative only. For upper molars, we took measurements (Fig. 2) analogous to those employed for tribosphenic therians (see Lillegraven 1969, fig. 5). Calculations, descriptive statistics, and tests were done with Systat version 7; original data are available from the senior author upon request.

Dental terminology is shown in Figure 3. The homologies of some of the upper molar cusps of spalacotheriids and other symmetrodonts – e.g., the presence of a metacone (Butler 1939; Patterson 1956) – are unclear, and the nomenclature is inconsistent. Most workers have referred to the three primary cusps of upper and lower molars in primitive mammals as A, B, and C; and a, b, and c, respectively (e.g., Crompton & Jenkins 1968; Cassiliano & Clemens 1979; Jenkins & Crompton 1979). Crompton (1971) regarded the metacone of tribosphenic Theria as a neomorph, and referred to the distolabial of the three primary upper molar cusps as cusp "c"; we follow convention in referring to this as cusp C, in order to avoid confusion with lower molar cusp c, though we point out that similar problems exist with this term, as upper molars of primitive marsupials and certain other tribo-

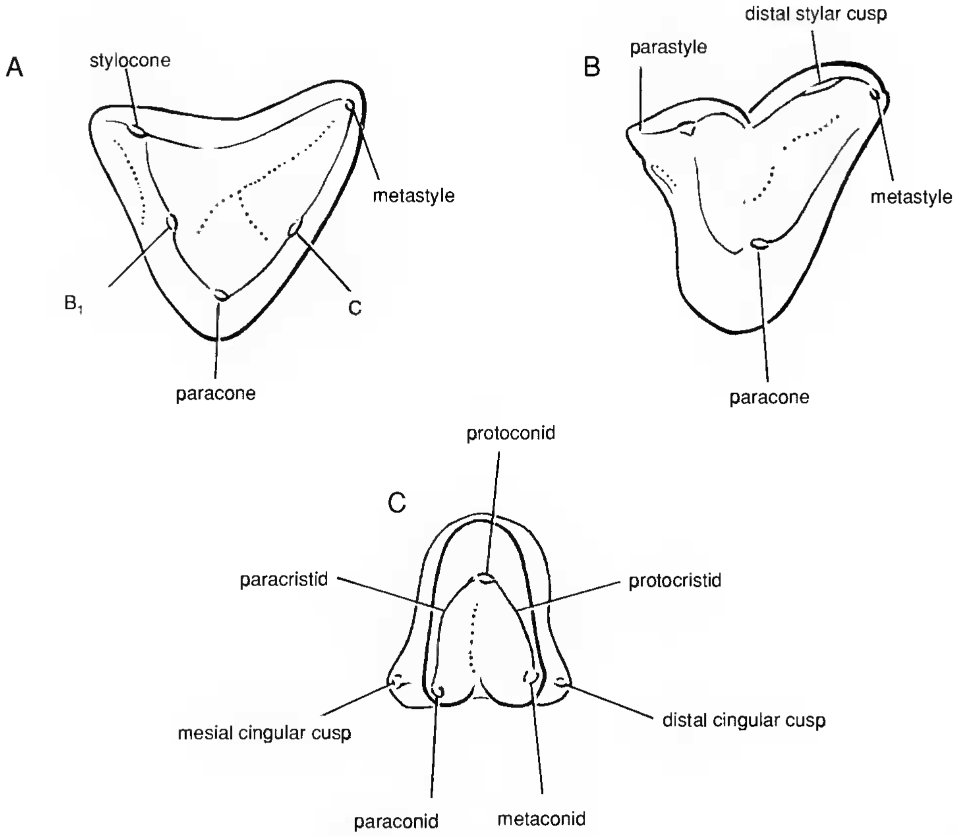

FIG. 3. — Dental terminology employed in this paper ; **A**, upper molar (M4) of *Spalacotherium* (modified after Simpson 1928a, fig. 34, and Patterson 1956, fig. 12); **B**, upper molar of *Spalacolestes*; **C**, lower molar of *Spalacolestes*.

sphenic mammals have a stylar cusp C (see Clemens 1979, we thank R. C. Fox for pointing this out to us). Other authors (Butler 1939; Patterson 1956; Kermack *et al.* 1968; Prothero 1981; Hopson 1997) interpret cusp C – which in spalacotheriids (where present) is located on the postparacrista about midway between the paracone and the distolabial corner of the tooth – as homologous with the tribosphenidan metacone. Following arguments presented by Sigogneau-Russell & Ensom (1998), we believe this to be probable, but follow Hu *et al.* (1998) in retaining the traditional nomenclature for spalacotheriids. Certain spalacotheriids also have an unusual cusp on the preparacrista, about halfway between the paracone and the mesolabial corner of the tooth, where a second cusp is generally present. We follow Patterson (1956) and Sigogneau-Russell & Ensom (1998) in regarding the latter cusp as the stylocone (see also Sigogneau-Russell 1991a), so that the cusp lingual to it (but labial to the paracone) is a neomorph. The most recently applied term for this cusp in the middle of the preparacrista is cusp B_1 (Hu *et al.* 1997), and this usage is adopted herein. Symmetrodont upper molars also commonly bear one or more cusps placed on the stylar shelf, distal to the ectoflexus (if one is present). That at the corner of the tooth may be termed, by convention, the metastyle. The more mesially placed cusp has been referred to as a posterior stylar cusp (e.g., Fox 1985) or, in analogy with the similarly placed cusp of tribosphenic therians (e.g., Simpson 1929; Clemens 1979; Fox 1984a), as stylar cusp D (e.g., Sigogneau-Russell 1991b; Sigogneau-Russell &

Ensom 1998). Unfortunately, the term "cusp D" has also been applied to the metastylar cusp (Hu *et al.* 1997). In order to avoid confusion with this usage or implied homology with the similarly-positioned cusp of marsupials, placentals, or therians of "metatherian-eutherian grade," we refer to the cusp placed on the stylar shelf, distal to the median part of the tooth but proximal to the metastyle (with which it should not be confused), as a "distal stylar cusp."

The medial surface of the dentary in mammals commonly bears a ridge, crest, or analogous structure, generally near or at the inferior margin and located posterior to the mandibular foramen, for attachment of the m. pterygoideus medialis. We are unable to find a standard anatomical term for this structure, and various names have been applied to it in the literature. Simpson (e.g., 1926, 1928a) alternatively referred to this structure as a "pterygoid crest" or "pterygoid ridge," sometimes using both terms in the same work (e.g., Simpson 1929). Recent authors (e.g., Rowe 1988) sometimes refer to it as a "pterygoid shelf," and this term has become standard for multituberculates (e.g., Miao 1988; Gambarayan & Kielan-Jaworowska 1995), in which the inferior margin of the dentary is strongly inflected lingually. In order to promote precision in usage and to avoid confusion in character state or implied homology (see discussion in Miao 1993), we refer to the structure in question simply as a "pterygoid crest," except where it is obviously developed into a shelf, as in multituberculates, or into an inflected angle, as in marsupials and some early Eutheria (see Sánchez-Villagra & Smith 1997, and below). At least, one of the species described herein is characterized by a pterygoid crest that bears a hypertrophied, process-like lingual extension that is unique, so far as we are aware. Lacking any standard term for this feature, we refer to it as a "pterygoid process."

ABBREVIATIONS FOR INSTITUTIONS CITED IN THE TEXT

BM	British Museum, London, UK;
UK	FMNH, Field Museum of Natural History, Chicago, Illinois, USA;
GI PST	Institute of Geology, Section of Palaeontology and Stratigraphy, Mongolian Academy of Sciences, Ulan Bator, Mogolian Peoples' Republic;
MNA	Museum of Northern Arizona, Flagstaff, Arizona, USA;
OMNH	Oklahoma Museum of Natural History, Norman, Oklahoma, USA;
UALVP	University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA;
YPM	Yale Peabody Museum, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

Order SYMMETRODONTA Simpson, 1925

COMMENTS. — This group was proposed by Simpson (1925a) to include then-known taxa (all thought to be Jurassic in age) having the three principal molar cusps arranged in a triangular pattern, thereby distinguishing them from the serially tricuspid triconodonts, with which they had been previously grouped (e.g., Osborn 1888, 1907). Symmetrodonta have long been conceived as a paraphyletic group (see, e.g., Patterson 1956; Cassiliano & Clemens 1979, fig. 7-4), but this simple picture became increasingly complex with the discovery of geologically older taxa, particularly Rhaeto-Liassic *Kuehneotherium* Kermack *et al.*, 1968 (see Kermack *et al.* 1968) and, later, *Woutersia* Sigogneau-Russell, 1983 (see Sigogneau-Russell 1983; Sigogneau-Russell & Hahn 1995). Mandibles referred to *Kuehneotherium*, at least, retain a postdentary trough and attachment facets for the postdentary elements seen in cynodonts and primitive mammals such as *Morganucodon* Kühne, 1949 and docodonts (Kermack & Mussett 1958; Kermack *et al.* 1968; Kermack *et al.* 1973; Lillegraven & Krusat 1991), and lack derived features (such as a pterygoid crest) found in other mammals, including some triconodonts (e.g., Rowe 1988; Wible 1991; Wible & Hopson 1993). Hence, either the mammalian middle ear complex or the "reversed triangle" pattern of upper and lower molars evolved independently more than once; both cases have been argued (see, e.g., Allin & Hopson 1992; Rougier *et al.* 1996). Prothero (1981) resolved this problem by excluding *Kuehneotherium* from Symmetrodonta (see also Hopson 1994), but his analysis did not include non-therian groups, and it is unclear how other, more recently described taxa (e.g., *Woutersia*, *Zhangheotherium* Hu *et al.*, 1997, *Thereuodon* Sigogneau-Russell, 1989, *Shuotherium* Chow & Rich, 1982, *Kotatherium* Datta, 1981, and a host of enigmatic taxa from the Campanian Los

Alamitos fauna of Argentina: see references cited above and Datta 1981; Chow & Rich 1982; Sigogneau-Russell 1989; Bonaparte 1990; Sigogneau-Russell 1991b; Prasad & Manhas 1997; Sigogneau-Russell & Ensom 1998) would fit into this scheme. The situation is further complicated by the fact that some molars of Amphilestidae, generally placed in the Triconodonta (e.g., Simpson 1945), have their principal cusps arranged in an obtuse triangle, and a relationship to Symmetrodonta has been suggested on this basis (Mills 1971; see also Jenkins & Schaff 1988; and discussion in Kielan-Jaworowska & Dashzeveg 1998). Fox (1985) proposed a trifold classification of Symmetrodonta, including Tinodontidae (containing *Kuehneotherium* and several other taxa, as well as *Tinodon*). *Kuehneotherium* has been shown to be highly similar to *Tinodon* (e.g., Crompton & Jenkins 1967), but its placement in the Tinodontidae is plagued by the same difficulty as its referral to Symmetrodonta in general: it retains an extremely primitive jaw structure, whereas in *Tinodon* the postdentary elements were evidently detached and a pterygoid crest is present (see Prothero 1981). We can offer nothing new to solve this dilemma and thus have not attempted to define or diagnose Symmetrodonta. However, there are some data to uphold integrity of the "core" group, Spalacotheriidae. Pending further analysis and, hopefully, more data from the fossil record, we find it useful to retain a traditional, inclusive concept of "symmetrodonts" (e.g., Cassiliano & Clemens 1979; Fox 1985). A recent, comprehensive discussion of the problem in defining Symmetrodonta, together with a thorough historical review of relevant taxa, is given by Sigogneau-Russell & Ensom (1998). McKenna & Bell (1997) distributed the contents of the Symmetrodonta among several higher groups within Mammalia, which they diagnosed primarily on the basis of detachment of accessory jaw bones (postdentary complex) from the craniomandibular joint and their association with the cranium as elements of the auditory apparatus. This arrangement implies a reversal for *Kuehneotherium* which, as noted, evidently retained a full complement of postdentary elements that were well integrated with the dentary.

Recently, the term "Theria" has been formally defined as a crown-based taxon restricted to the common ancestor of marsupials, placentals, and all of its descendants (Rowe 1988). Herein we follow a more traditional, informal concept that also includes "Theria of metatherian-eutherian grade," peramurans, eupantotheres, and symmetrodonts (e.g., Patterson 1956), in recognition of the current instability in phylogenetic interpretation of the major groups of mammals.

Family Spalacotheriidae Marsh, 1887

Type genus. — *Spalacotherium* Owen, 1854.

Included genera. — The type, and *Spalacotheroides* Patterson, 1955; *Symmetrodontoides* Fox, 1976; *Spalacotheridium* Cifelli, 1990; *Microderson* Sigogneau-Russell, 1991; *Zhangheotherium* Hu *et al.*, 1997; and *Spalacolestes*, n. gen.

Distribution. — ?Late Jurassic through Early Cretaceous, western Europe (Clemens 1963; Clemens & Lees 1971; Krebs 1985); Early through Late Cretaceous, North America (Patterson 1955; Fox 1976); Late Jurassic or Early Cretaceous, Asia (Hu *et al.* 1997); ?Early Cretaceous, northern Africa (Sigogneau-Russell 1991b). *Spalacotherium* was first described from the Purbeck beds, traditionally regarded as Upper Jurassic (see discussion in Clemens *et al.* 1979). Recent literature increasingly refers the mammal-bearing part of the Purbeck to the Berriasian (Lower Cretaceous, see Allen & Wimbledon 1991; Kielan-Jaworowska & Ensom 1994; Sigogneau-Russell & Ensom 1994; Ensom & Sigogneau-Russell 1998).

Revised diagnosis. — Symmetrodonts with lower molars bearing well-developed primary cusps (paraconid, protoconid, metaconid) arranged in an acute angle, a reduced talonid; five lower molars present in *Zhangheotherium*, increasing to six or more, where known, in other taxa. Unique pattern of interlocking for lower molars, whereby the distal cingular cusp of one molar is placed labial to the mesial cingular cusp of the succeeding tooth. Upper molars primitively with accessory cusp (B_1) on preparacrista between paracone and stylocone.

Comments

A more detailed diagnosis of Spalacotheriidae was given by Fox (1985), based on then-known taxa: *Spalacotherium*, *Spalacotheroides*, and *Symmetrodontoides*. The concept of the family is broadened here to include *Zhangheotherium*, recently described from the Late Jurassic or, more probably, Early Cretaceous of China (Hu *et al.* 1997). By comparison to remaining spalacotheres, *Zhangheotherium* would appear to be primitive in some respects, such as the lower number of molars, ?lack of continuous mesial and distal shearing surfaces on molars (upon eruption), and, perhaps, features on the medial side of the dentary (see below). In other respects, such as the complete lack of cingula on the lower molars, *Zhangheotherium* is strikingly atypical. Nonetheless, molar morphology is otherwise similar to that of *Spalacotherium*, particularly in the presumably derived features cited in the diagnosis. We tentatively follow Hu *et al.* (1997) in referring *Zhangheotherium* to the Spalacotheriidae. Cusp B_1 is present in *Spalacotherium* (e.g., Clemens 1963), *Spalacotheroides* (see Patterson 1956), and *Zhangheotherium* (see Hu *et al.* 1997), the geologically oldest and, for reasons detailed below, considered by us to otherwise be the most primitive members of the family. We therefore tentatively regard the presence of cusp B_1 to be primitive for (and diagnostic of) Spalacotheriidae. Sigogneau-Russell & Ensom (1998) considered the loss of Crompton (1971)'s facet A as characterizing Spalacotheriidae. It is presently uncertain as to whether or not facet A is seen in *Zhangheotherium*, and this feature has accordingly been omitted from the diagnosis, pending detailed description of that taxon.

Microderson, represented by a single tooth belonging to the type and only species, *M. laaroussii* Sigogneau-Russell, 1991, from the Early Cretaceous of Morocco, was initially described as a spalacotheriid (Sigogneau-Russell 1991b), but its pertinence to the family has recently been called into question (Sigogneau-Russell & Ensom 1998). We tentatively include it here for the sake of completeness but, because it is poorly known and of enigmatic affinities, make only passing reference to it in the comparisons below.

Given the low known diversity of symmetrodonts and their meager representation in the fossil record, it comes as somewhat of a surprise that several species, collectively represented by more than 250 specimens, are present in the Mussentuchit local fauna. Most of these specimens are isolated teeth, many of which are worn or incomplete. This, coupled with the facts that the species are quite similar to each other and to named taxa from North America, that the tooth rows include many molars (probably seven in the lower series and six in the upper series) that are rather simple and vary in only subtle ways from one position to the next, and that no closely similar taxon is known by anything close to a complete dentition, makes identification of taxon and tooth position less than straightforward (see also Mills 1984). We gave first consider-ation in our analyses to the lower molar series for several reasons. First, the sample of lower molars is comparatively large, thus permitting statistical treatment and some appraisal of variability. Second, the most morphologically informative specimens, both from the Cedar Mountain Formation and elsewhere (e.g., Fox 1976), are dentigerous mandibular fragments. A final, most compelling reason for giving primary consider-ation to the lower molars is that the holotypes of all spalacotheriid symmetrodonts (except *Microderson*) include lower molars, and most species are based on lower molar series or individual teeth.

The less numerous upper molars were then assigned to lower molar taxa based on size and morphological considerations, and were sorted to locus (see below). Judged from the composition of the Mussentuchit local fauna (Cifelli *et al.* 1997, 1999) and comparison with *Spalacotherium* (see Simpson 1928a), spalacotheriid premolars are clearly present in the existing collection. No attempt was made to sort these according to taxon, however, because of the difficulties posed by assignment to locus; hence, only the molar dentition is considered herein.

LOWER MOLARS

Fortunately, one of the taxa from the Cedar Mountain Formation is known by a relatively enormous sample; several jaws are included, and as a result the last four molar loci of the mandibular dentition are represented by teeth in place. A dentary fragment preserving the anterior part of the molar series, including three loci, is known for the closely similar *Symmetrodontoides canadensis* (see Fox 1972, 1976). These specimens, together with comparison to the complete dentition of the somewhat more divergent *Spalacotherium* (see Simpson 1928a; Clemens 1963), provide the foundation for evaluating position of isolated teeth on the basis of relative crown height, differences in the proportions of the lingual cusps (paraconid, metaconid), acuteness of the trigonid angle, configuration of the lingual cingulum, width to length proportions, and other considerations.

Once the lower molars were sorted to their relative and approximate positions in the tooth row, it became apparent that three diagnosable species, differing in size (Fig. 4) and morphology, were

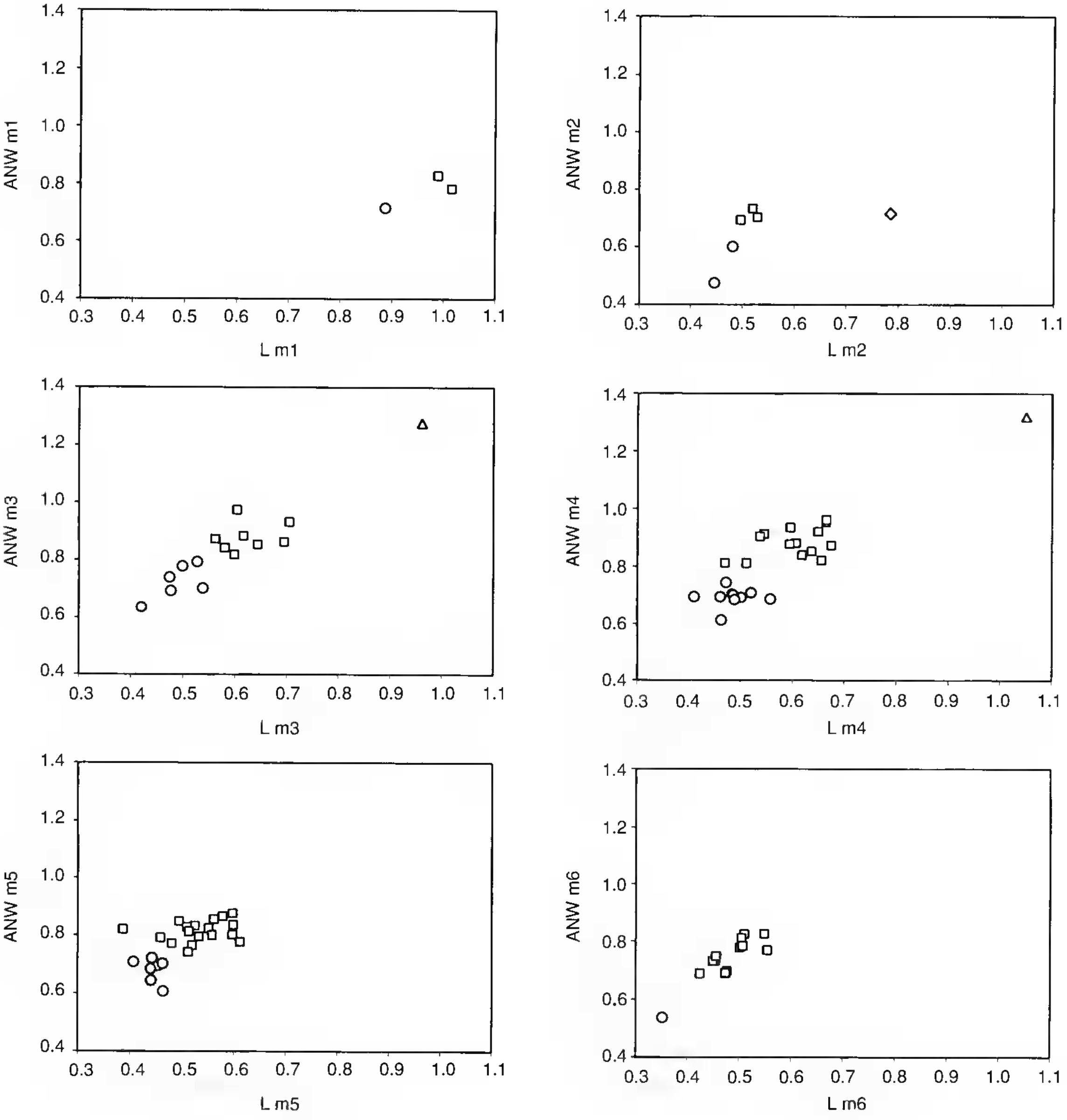

FIG. 4. — Bivariate scatterplots for lower molar length (**L**) and width (**ANW**) of Spalacotheriidae from the upper Cedar Mountain Formation by inferred tooth locus. Symbols: **circles**, *Spalacotheridium noblei* n. sp.; **squares**, *Spalacolestes cretulablatta* n. gen., n. sp.; **triangles**, *Spalacolestes inconcinnus* n. gen., n. sp.; **diamond**, gen. and sp. indet.

present in the sample: the well-represented taxon just mentioned, known by several jaws and nearly 100 isolated molars; a smaller species, represented by about 35 isolated teeth; and a larger species, for which only three lower molars are known. One problematic specimen evidently represents a fourth, unidentified taxon. For the species represented by the largest sample, it was then possible to conduct detailed comparisons in order to identify tooth locus more precisely, evaluate variability at each tooth position and differences between adjacent teeth (in terms of their measurements), and estimate the molar count. These results were then used for refinement of identifications for the other species. Description of the results is deferred to the individual species accounts, but some prefatory comments are warranted here because of the need to provide a basis for comparison with previously described species, and the implications of the results presented herein for interpretation of tooth position among specimens referred to those species.

As mentioned, the best-represented spalacotheriid of the Mussentuchit local fauna is known by the last four lower molars in place, as well as by a large sample of isolated teeth. Except for the last molar, which is morphologically distinctive, it is not possible to identify positions of individual posterior molars with certainty because of overlapping ranges of variation between loci. Nonetheless, the isolated molars fall into recognizable clusters corresponding to known tooth positions, and we consider our identifications to be probable, with mistaken identity by more than one tooth position being unlikely.

Among the isolated teeth representing anterior molar loci, one group is consistently and clearly recognizable. Based on known trends in the dentition of spalacotheriids (e.g., Simpson 1925b, 1928b; Clemens 1963; Fox 1976), these teeth can be confidently identified as m1. The teeth that are morphologically intermediate between this first molar and the anteriormost of those in known tooth positions fall into two clusters, recognizable on the basis of both qualitative and quantitative characteristics. Again, however, because of overlapping ranges of variability, individual teeth can be identified with probability, not certainty, according to position. Hence the available data indicate that, in this species at least, seven lower molars were present. Rather than using quotation or question marks on the numerous specimens cited below, we simply call attention to the facts that a complete dentition of a North American spalacotheriid remains unknown and that, in any case, identification of isolated molars (except the first and last, which are morphologically distinctive) cannot be established unambiguously, even with complete specimens at hand for comparison. The identifications of teeth to respective loci should be regarded as tentative.

Of the remaining spalacotheriids from the Mussentuchit local fauna, comparison with the taxon just mentioned indicated that a second species is represented by teeth recognizable as belonging to the first six lower molar positions; these will be referred to as m1-6. It is unclear as to whether an m7 was lacking in this species, or is not represented in existing collections. The third diagnosable species is known by only three lower molars, each recognizable as to locus with the same confidence as the morphologically similar, best-represented species.

Among described species of North American Spalacotheriidae, the best known is *Symmetrodontoides canadensis*, the holotype of which (UA 8588) consists of an incomplete jaw with three teeth. These were identified by Fox (1976) as probably representing m3-5. The basis for this identification was a referred specimen, UA 12086, a mandibular fragment with a molariform tooth considered to be m1. The tooth of UA 12086 has a broadly obtuse trigonid angle that, if compared to UA 8588, would form a graded series with the teeth on the latter specimen, assuming that an unrepresented tooth position intervened between the two specimens. Dentigerous jaws and numerous isolated teeth similar to that of UA 12086 are known from the Cedar Mountain Formation, and work in progress by one of us (RLC) indicates that these are not lower molars of spalacotheriids. Comparison of UA 8588 to the extensive series mentioned above indicates that the teeth in this specimen are m1-3. Fox (1976) also referred an isolated molar, UA 12087, to *Symmetrodontoides canadensis*. As demonstrated by Fox, this tooth clearly represents a more posterior tooth locus. Consideration of the proportional differences between this specimen and m3 of the holotype, together with the large sample from the Cedar Mountain Formation, suggests that UA 12087 probably is an m5 or, as Fox (1976) suggested, m6.

Other species are known by isolated teeth only, and identification of tooth position is more problematic. The first symmetrodont to be described from the Cretaceous of North America is *Spalacotheroides bridwelli*, from the Aptian-Albian of the Trinity Group, Texas. *S. bridwelli* was based on a mandibular fragment with a single lower molar (Patterson 1955); several upper molars were later referred to the species (Patterson 1956). Patterson (1955) suggested that, as with *Spalacotherium*, *Spalacotheroides* probably had seven molars, and that the tooth in the holotype (FMNH PM 933) is the antepenultimate – i.e., m5. Fox (1976) indicated that this tooth best matches the second tooth on the holotype of *Symmetrodontoides canadensis*, then identified as m3 or 4 and considered herein to be m2. We concur: in terms of size and overall morphology, we find FMNH PM 933 to be most similar to m2 or 3 of *Symmetrodontoides*. However, the paraconid on FMNH PM 933 is lacking. For this reason, and because tooth locus cannot be reasonably hypothesized without other specimens belonging to the same species, the lower dentition of *Spalacotheroides bridwelli* must be set aside from comparisons for the time being. This species is said to differ from *Spalacotherium* (see Patterson 1955) and all other Spalacotheriidae (Fox 1976) except *Zhangheotherium* in having an incomplete labial cingulum. No other lower molars are yet known for *S. bridwelli*. A somewhat more obtuse-angled tooth (perhaps m1), comparable in size and overall gestalt to FMNH PM 933, is now known from the Cloverly Formation (RLC, unpublished data), which is approximately equivalent in age to the part of the Trinity Group that produced *Spalacotheroides* (Jacobs *et al.* 1991). Unfortunately, the labial side of this tooth is damaged, leaving open the question of whether or not the cingulum was complete.

Three species of Spalacotheriidae have been described from the Upper Cretaceous of southern Utah. *Symmetrodontoides foxi* Cifelli & Madsen, 1986, from the Wahweap Formation (assumed to be lower Campanian and approximately equivalent to the upper Milk River Formation, Alberta, which produced *S. canadensis*), was based on presumed m4 (MNA 4589, the holotype) and a referred tooth (MNA 4522) assumed to represent m7 (Cifelli & Madsen 1986). A new specimen of this species, together with comparison to the extensive series representing a morphologically similar species from the Cedar Mountain Formation, suggests that MNA 4589 is an m2 and that MNA 4522 is m6 (or, less probably, m5); m4 of *S. foxi* is represented by OMNH 20135.

The Smoky Hollow Member of the Straight Cliffs Formation, late Turonian in age (Eaton 1991), has yielded two spalacotheriids (Cifelli 1990). The present comparisons, which include new materials, indicate that the holotype of *Symmetrodontoides oligodontos* Cifelli, 1990 (MNA 5789) is probably m6 (not m7 as originally thought), and that the original referred specimen (OMNH 20381) represents m4. Newly-referred specimens include MNA 6047 and 6755, tentatively identified as m2 and m4, respectively; and 29523, a mandibular fragment with m2. The holotype of the diminutive *Spalacotheridium mckennai* Cifelli, 1990 is most probably m2 (not m4 as originally believed); newly-referred OMNH 29524, MNA 6046, and OMNH 29526 are probably m1, m4, and corroded m6, respectively.

UPPER MOLARS

The upper molars are evidently much more fragile and subject to breakage during the screenwashing process: the sample from the Cedar Mountain Formation includes only 54 catalogued upper molars, as opposed to more than 200 lowers. Of these, 45 upper molars proved assignable to species but only 31 were formally included in hypodigms because of their greater completeness; statistical analysis was precluded by insufficient samples. With one exception (described under ?Spalacotheriidae, indet.), the upper molars readily fell into three categories on the basis of size, as had been established for the lower molars. Within species, there is variation that is clearly due to tooth locus. Trends known for symmetrodonts represented by dentulous jaws (e.g., *Spalacotherium*, *Zhangheotherium*, see Simpson 1928b; Clemens 1963; Hu *et al.* 1997), together with molars (Fox 1985) of a species similar to those from the Cedar Mountain Formation, provided the basis for establishing which teeth were more anteriorly placed in the jaw, and which of these represented the first molar. For the most abundant species, it was then possible to sort molars into discrete morphological categories, and to document progressive changes through the upper series. We recognize six morphological categories among upper molars of this species, and therefore tentatively regard the upper molar count as six. This accords with the fact that, in the lower dentition, where we believe seven molars are present, m7 is reduced and has a prevallid (for shearing against the distal face of M6) but no postvallid surface. A differential molar count between upper and lower jaws is not wholly unexpected, as the condition is known to occur in the primitive spalacotheriid *Zhangheotherium* (see Hu *et al.* 1997). Simpson (1928a) regarded the upper dentition of *Peralestes* (which we include in *Spalacotherium*) as having seven molars. Clemens (1963) later showed that only six were present on one specimen, at least; it is possible that molar count varied in this taxon.

Identification of upper molars belonging to the most abundant species then served as the basis for identifying loci among isolated teeth referable to the less abundant taxa from the Cedar Mountain Formation, and for morphologically similar species from elsewhere. Fox (1985) referred two upper molars to the Aquilan spalacotheriid *Symmetrodontoides canadensis* and indicated that one probably represents a more posterior locus than the other. We find this indeed to be the case, our comparisons suggesting that UALVP 16271 is M1 or 2 and UALVP 16272 is M2 or 3 of this species. No upper molars have yet been described for symmetrodonts from southern Utah, but materials in hand suggest that the following are represented: *Symmetrodontoides foxi*, M4 (MNA V4653); *S. oligodontos*, M1 (OMNH 29525), M2 (MNA V6048, OMNH 29040), and M6 (OMNH 29039); *Spalacotheridium mckennai*, M5 (MNA V6756). Other spalacotheriids for which isolated upper molars have been described are problematic because only single teeth (rather than series) are available, and they are so different from the taxa considered here as to be non-comparable. Several isolated upper molars have been referred to *Spalacotheroides bridwelli*. Of these, FMNH PM 1235 is relatively long mesiodistally and probably represents an anterior position, as indicated by Patterson (1956, fig. 1). A cast of FMNH PM 1133, which is just a fragment of a tooth, suggests that this may have been a more posterior molar. The upper molar series is known for *Zhangheotherium*; however, the preliminary description and available illustration (which shows the upper molars in an oblique orientation, Hu *et al.* 1997, fig. 2) permit only cursory comparisons with remaining spalacotheriids. The remaining taxon possibly referable to Spalacotheriidae and represented by an isolated upper molar is *Microderson laaroussii*, from the Early Cretaceous of Morocco. As recognized by Sigogneau-Russell (1991b), this tooth is so dissimilar to upper molars of *Symmetrodontoides* (and, by implication, to remaining taxa considered here) that we cannot hazard a guess as to its position in the jaw.

SPALACOLESTINAE n. subfam.

TYPE GENUS. — *Spalacolestes*, n. gen.

INCLUDED GENERA. — The type, and *Spalacotheroides* Patterson, 1955, *Symmetrodontoides* Fox, 1976, and *Spalacotheridium* Cifelli, 1990.

DISTRIBUTION. — Cretaceous (Aptian-Albian through early Campanian), North America.

DIAGNOSIS. — Distinguished from primitive spalacotheriids (*Spalacotherium*, *Zhangheotherium*) in possessing the following derived features: molars more acutely angled; anterior upper molars with strong parastyle; upper molars with preparacrista lower than postparacrista and with distal stylar cusp present, proximal to the metastyle. Pterygoid crest and pterygoid fossa, where known (*Spalacolestes*, *Spalacotheroides*) extend anterodorsally from mandibular foramen toward alveolar margin of dentary.

COMMENTS. — As shown by the comparisons below, there is good reason to believe that the North American Cretaceous spalacotheriids form a monophyletic assemblage with respect to remaining members of the family. We formalize this relationship by placing the North American taxa in their own subfamily, named for the best known genus (described below). Within the subfamily, poorly known *Spalacotheroides* is the oldest and appears to retain the greatest number of primitive features. The remaining genera of Spalacotheriidae (*Spalacotherium*, *Zhangheo-*

therium), not treated in detail herein, are relegated, by default, to Spalacotheriinae (Marsh 1887), n. rank, which current evidence suggests may be paraphyletic (see below).

Spalacolestes n. gen.

Type species. — *Spalacolestes cretulablatta* n. sp.

Included species. — The type, and *S. inconcinnus* n. sp.

Etymology. — *Spalax* (Greek), mole, and a commonly used prefix for genera of this family; *lestes* (Greek), robber, plunderer, and a commonly used suffix for genera of small and presumably stealthy, predaceous mammals.

Distribution. — Albian-Cenomanian, western United States.

Diagnosis. — Differs from *Spalacotherium* in having more acutely angled trigonids on posterior molars and in having lower molar paraconid much lower than metaconid. Differs from *Symmetrodontoides* in having proportionately narrower posterior lower molars with more obtusely-angled trigonids and lesser height differential between paraconid and metaconid; m1 differs from that of *Symmetrodontoides* in having lower, more conical paraconid and lower paractistid. Lower molars differ from those of *Spalacotheridium* in having a more pronounced height differential between paraconid and metaconid. Upper molars similar, where known, to those of *Symmetrodontoides*, except that M1-2 have a more bulbous-based paracone with a gently curving (not tightly arced or folded) lingual face. Upper molars differ from those of *Spalacotheroides* and primitive taxa in reduction of the stylocone, lack of cusps B_1 and C, presence of an extremely low preparactista (anterior loci only), and presence of an enlarged distal stylar cusp. Differs from the otherwise similar *Spalacotheridium* in having deeper trigon basins and, on posterior upper molars, parastyle reduced.

Spalacolestes cretulablatta n. sp.
(Figs 6-11)

Holotype. — OMNH 29600, right dentary with m4-7.

Hypodigm. — The holotype, and the following specimens:
Jaws: dentary with m4-5, OMNH 27421; dentary with m6, OMNH 27557.
Lower molars: **m1**, OMNH 26424, 26425, 26697, 29608, 30621, 33044, 33220; **m2**, OMNH 27451, 27511, 27541, 32947, 33045, 33054, 33226, 33898; **m3**, OMNH 26698, 27591, 27631, 33047, 33217, 33851; **m4**, OMNH 26419, 26420, 26422, 26704, 26708, 27471, 27484, 27630, 30627, 30628, 30631, 33055, 33225, 33901; **m5**, OMNH 26423, 26695, 26703, 26706, 26707, 27462, 29603, 29606, 30619, 30620, 33037, 33042, 33043, 33049, 33050, 33222, 33905; **m6**, OMNH 27425, 27464, 27569, 29601, 29767, 30622, 30625, 33040, 33046, 33048, 33218, 33228; **m7**, OMNH 27463.
Upper molars: **M1**, OMNH 26426, 33233; **M2**, OMNH 26686, 29611, 32897; **M3**, OMNH 27512, 33060; **M4**, OMNH 26688, 26693, 30611, 30612, 33057, 33231; **M5**, OMNH 25796; **M6**, OMNH 26691, 30614, 32949.

Additional referred specimens. — Incomplete upper molars, locus uncertain: OMNH 25795, 26427, 26430, 27632, 33056, 33058, 33059, 33235, 33237, 33906, 33907.

Localities and horizon. — OMNH localities V235, V239, V695, V794, and V868 (Fig. 1); upper part of Cedar Mountain Formation; Albian-Cenomanian.

Etymology. — *Cretula* (Latin, dim. of *creta*), chalk; *blatta* (Latin), cockroach. Allusion is to the Cretaceous age and remarkable, roach-like abundance of the species.

Diagnosis. — The smaller of the two species referred to the genus. Differs from the slightly smaller *Symmetrodontoides oligodontos* in characters noted for generic diagnosis and in having less slender, anteroposteriorly compressed lower molar para- and metaconids. Differs from *S. foxi* and *S. canadensis* in generic charactets and in being much smaller.

Comments and description

Lower molar series

Spalacolestes cretulablatta n. gen., n. sp. is the most abundant therian mammal of the Mussentuchit local fauna and is represented by 94 specimens of the lower molar series. Of these, the holotype preserves the last four molars in place, and two other dentulous jaws have teeth of known position in the posterior part of the series. Isolated teeth not referable to these loci can be sorted into three groups based on crown height, relative height and position of the paraconid, curvature of the lingual cingulum, and other characteristics. Standard measurements for these teeth (Table 1) also group into distinct clusters; as noted above, we therefore recognize seven lower molars. The most morphologically

TABLE 1. — Descriptive statistics for lower molar measurements (mm) of *Spalacolestes cretulablatta* n. gen., n. sp. See Figure 2 for measurement abbreviations and conventions.

	L	ANW	Pad-med	Prd-med	Angle
m1					
N	2	7	2	3	2
Range	0.989-1.016	0.750-0.856	0.730-0.750	0.559-0.716	61.771-68.440
Mean	1.002	0.801	0.740	0.652	65.106
CV	0.019	0.052	0.019	0.126	0.072
m2					
N	3	4	4	3	3
Range	0.496-0.529	0.694-0.752	0.431-0.444	0.415-0.480	45.600-50.309
Mean	0.515	0.721	0.437	0.448	48.163
CV	0.033	0.037	0.015	0.073	0.049
m3					
N	8	10	8	8	7
Range	0.562-0.705	0.809-0.975	0.369-0.552	0.498-0.663	42.738-48.260
Mean	0.626	0.878	0.473	0.562	45.950
CV	0.083	0.059	0.113	0.099	0.051
m4					
N	14	16	11	12	11
Range	0.470-0.675	0.736-0.963	0.359-0.472	0.496-0.598	29.714-40.046
Mean	0.601	0.868	0.413	0.598	35.068
CV	0.106	0.075	0.087	0.086	0.094
m5					
N	18	19	12	14	10
Range	0.387-0.612	0.742-0.876	0.362-0.469	0.501-0.610	34.071-40.857
Mean	0.533	0.811	0.406	0.563	37.656
CV	0.107	0.046	0.085	0.055	0.063
m6					
N	13	14	9	8	7
Range	0.381-0.555	0.651-0.826	0.288-0.424	0.402-0.630	31-920-37.643
Mean	0.480	0.749	0.347	0.522	34.239
CV	0.101	0.072	0.117	0.134	0.059
m7					
N	2	2	0	0	0
Range	0.383-0.410	0.484-0.487	–	–	–
Mean	0.396	0.485	–	–	–
CV	0.048	0.004	–	–	–

distinctive molars, identified as m1, have a low, anteriorly placed paraconid, somewhat lower crown in general, low crown width to length ratio, and wide trigonid angle (greater than 60°). The second and third lower molars are progressively shorter, wider, and taller crowned, with a more acute trigonid angle (Table 1; Figs 4-5) and bases of paraconid and metaconid more closely approximated; differences in means for dimensions of m2 and m3 are significant at the p = 0.05 level, whereas that for the trigonid angle is not (Table 2). These trends are continued through the fourth molar; the differences in width and length are not significant between m3 and m4, whereas that for the trigonid angle is: m4 has a much more acute angle (Tables 1, 2). The fifth lower molar is nearly as tall as m4, but tooth length and width decrease past m4, and the differences between means are highly significant. Values for trigonid angle overlap considera-

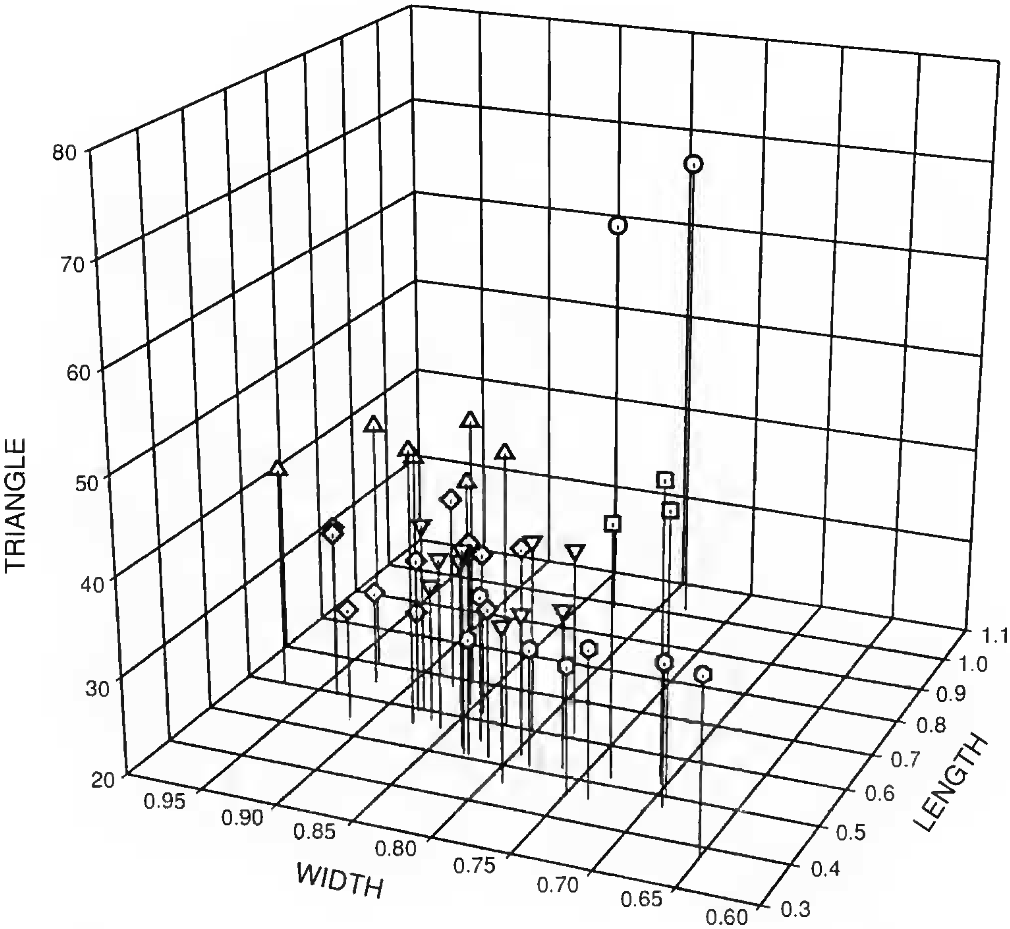

FIG. 5. — Proportional differences (length, width, trigonid angle) according to tooth locus for lower molars of *Spalacolestes cretulablatta*, n. gen., n. sp. Symbols: **circles**, m1; **squares**, m2; **upward pointing triangles**, m3; **diamonds**, m4; **downward pointing triangles**, m5; **hexagons**, m6 (m7 is omitted because it lacks a metaconid and the trigonid angle cannot be calculated).

bly between m4-6 (see comments above), and no consistent pattern is recognizable. On posterior molars, there is a tendency for the paracristid to be slightly longer than the protocristid, whereas the reverse is true for *Symmetrodontoides*. The sixth lower molar is lower crowned and smaller than m5. The last lower molar, m7, is lower crowned yet and is by far the smallest in the series. The metaconid on this tooth is lacking from OMNH 29600 (the holotype) and from one isolated, referred specimen. We consider it unlikely that presence of the cusp is variable within the species, given the distinctiveness of m7, although it is curious that so few molars assignable to this locus were recovered, in view of the large samples of more mesial teeth. The lack of a functional postvallid surface on m7 suggests that, as in *Zhangheotherium* (see Hu *et al.* 1997), *Spalacolestes cretulablatta* had one fewer molar in the upper than lower series. Changes in proportions and trigonid angle through the molar series are summarized in Figure 5, and a composite restoration is shown in Figure 6C, D.

All lower molars are double-rooted. None of the isolated teeth preserves both roots intact, but comparison within this sample, together with preserved alveoli on the jaw fragments assigned to *Spalacolestes cretulablatta*, indicates that the

TABLE 2. — Two-sample *t* test (independent *t* test) comparing mean measurements for adjacent lower molars, *Spalacolestes cretulablatta* n. gen., n. sp. First and last molars omitted because of insufficient data (N for samples are given in Table 1).

	Length	Width	Pad-med	Prd-med	Angle
m2 vs. m3					
Difference between means	0.111	0.157	0.035	0.114	2.213
Pooled variance *t*	- 3.514	- 5.664	- 1.111	- 3.228	1.371
Degrees of freedom	9	12	9	9	8
Probability	0.007	0.000	0.295	0.005	0.208
m3 vs. m4					
Difference between means	0.024	0.011	0.060	0.035	10.882
Pooled variance *t*	0.911	0.437	2.935	-1.460	7.568
Degrees of freedom	20	24	17	18	16
Probability	0.080	0.061	0.009	0.016	0.000
m4 vs. m5					
Difference between means	0.068	0.057	0.007	0.035	2.588
Pooled variance *t*	3.195	3.238	0.487	2.135	-2.041
Degrees of freedom	30	33	21	24	19
Probability	0.003	0.003	0.631	0.043	0.055
m5 vs. m6					
Difference between means	0.053	0.062	0.058	0.041	3.418
Pooled variance *t*	2.685	3.899	3.554	1.887	3.097
Degrees of freedom	29	31	19	20	15
Probability	0.012	0.000	0.002	0.074	0.007

roots were subequal in size (except for m7, in which the distal root is smaller) and mesiodistally compressed, with a characteristic subrectangular cross section that makes edentulous spalacolestine mandibles easily recognized as such. The cingulum is complete on all lower molars and is especially strong on the lingual side of m1 (Fig. 7A, B), where it shows almost no flexure; on subsequent molars, it flexes dorsally between the bases of paraconid and metaconid. The cingulum descends considerably as it extends past the interstitial regions of the tooth, so that the labial part of the crown is much higher than the lingual side. Mesiolingual and distolingual cuspules are present on the cingulum, as they are in other North American Spalacotheriidae; these are variable but are generally salient, projecting somewhat mesially and distally (as well as dorsally) from the cingulum. The paraconid and metaconid of m1 (Fig. 7A, B) have conical, well-separated bases when viewed lingually; the metaconid is about two-thirds the height of the protoconid, whereas the paraconid is less than one-half the height of that cusp when the tooth is viewed lingually. On m2 (Fig. 7C, D), the trigonid angle is more acute, and the bases of paraconid and metaconid are more closely approximated because the former cusp is more posteriorly placed. The paraconid is relatively taller than on m1, but lower than on succeeding molars. The metaconid of m2 is more slender, with a less robust base, than on m1. The lingual cingulum develops a pronounced lingual flexure on m3 (Fig. 7E, F), and this continues on succeeding molars. The labial face of the protoconid on this and succeeding teeth is less rounded and more sharply folded than on m1-2; the metaconid is nearly as tall as the protoconid, with the paraconid being only about half as tall as the protoconid, viewed lingually. Of the two basal cuspules, the distal (i.e., talonid) tends to be the more prominent and projecting; the succeeding tooth fits into the concavity of the distal cingulum formed labial to the distal cingular cusp (see Fox 1976). By m4 (Figs 7G, H, 8, 9), the bases of paraconid and metaconid are appressed, with a more slender, anteroposteriorly compressed appearance than on anterior teeth, when viewed

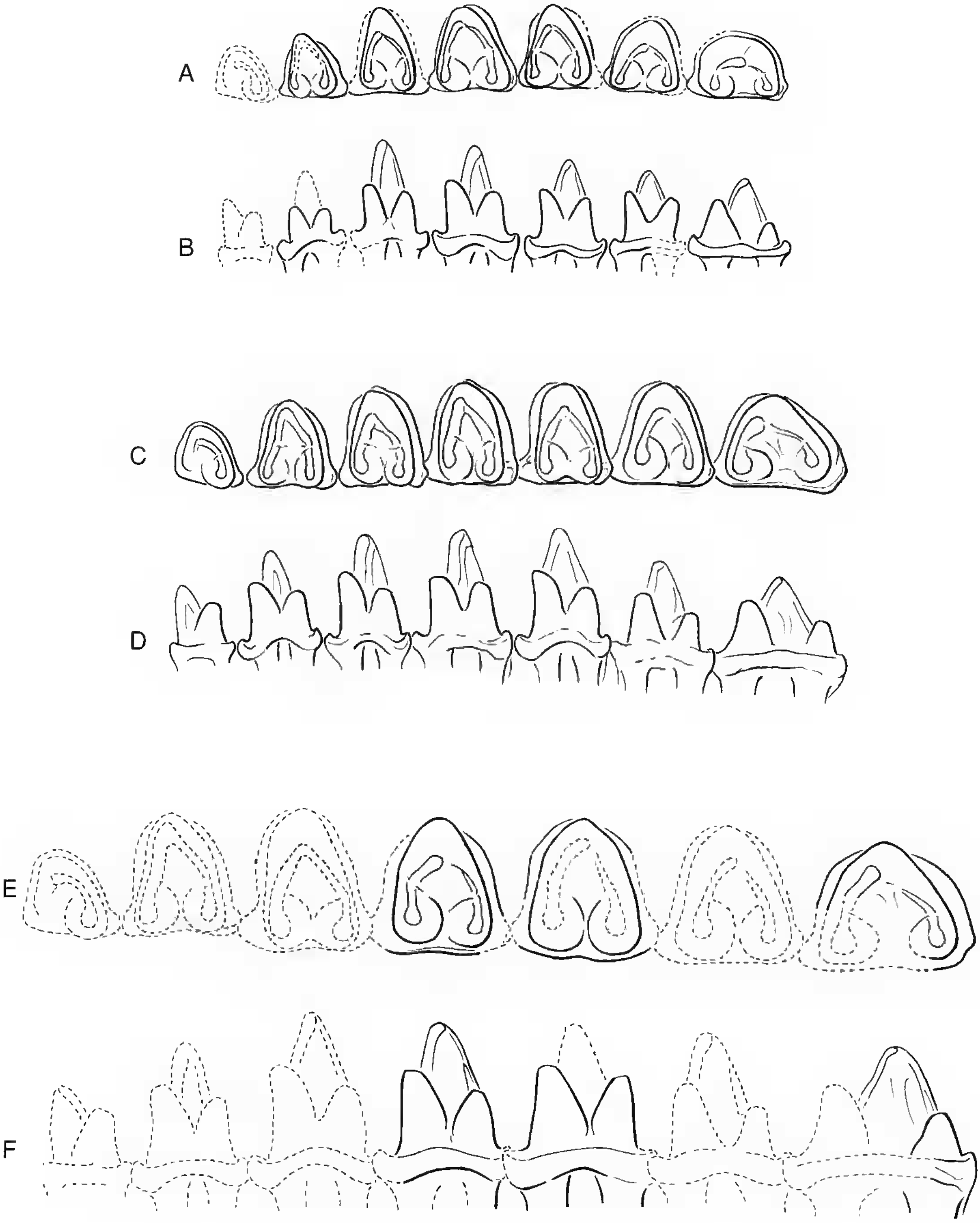

FIG. 6. — Composite lower molar series in occlusal (A, C, E) and lingual (B, D, F) views; **A**, **B**, *Spalacotheridium noblei* n. sp.; **C**, **D**, *Spalacolestes cretulablatta* n. gen., n. sp.; **E**, **F**, *Spalacolestes inconcinnus* n. gen., n. sp. Tooth series scaled to relative size.

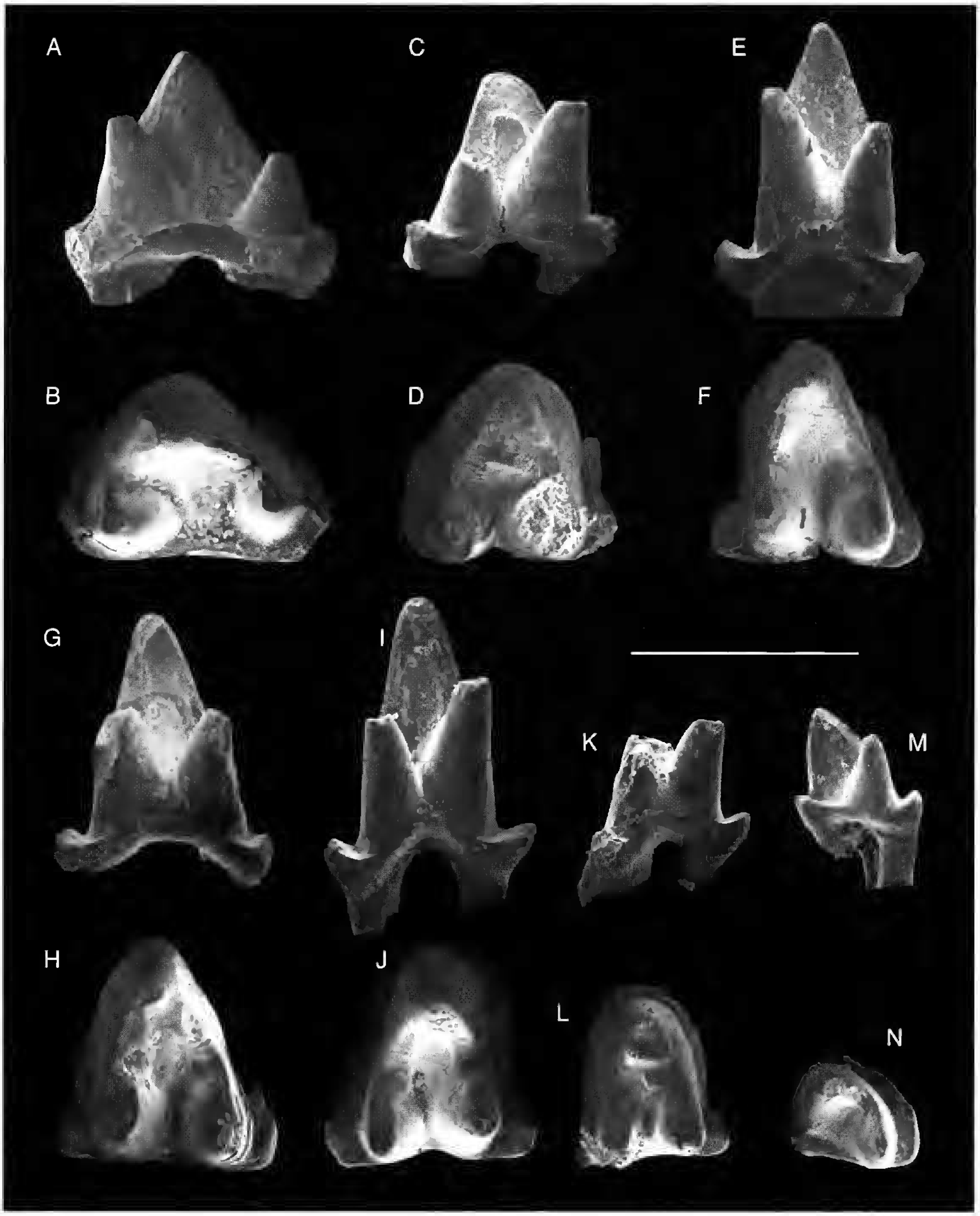

FIG. 7. — Scanning electron micrographs, lower molars of *Spalacolestes cretulablatta* n. gen., n. sp.; A, C, E, G, I, K, M, lingual views; B, D, F, H, J, L, N, occlusal views; **A**, **B**, left m1 (OMNH 26424); **C**, **D**, right m2 (OMNH 33226); **E**, **F**, left m3 (OMNH 33851); **G**, **H**, left m4 (OMNH 26422); **I**, **J**, right m5 (OMNH 30631); **K**, **L**, right m6 (OMNH 27557); **M**, **N**, left m7 (OMNH 27463). Jaw fragments and roots eliminated where needed to improve clarity. Scale bar: 1 mm.

lingually. Lower molars 5 and 6 (Figs 7I-L, 8) are similar, but progressively smaller, with crown height decreasing after an apparent maximum at m4-5. The last lower molar (Figs 7M, N, 8) is distinctive in its much smaller size; although it is two-rooted like more anterior teeth, the metaconid and protocristid are lacking, and the distal cingulum is expanded. The posteriormost molar (m7) of *Spalacotherium* is also quite small, but it retains a full complement of trigonid cusps (see Clemens 1963).

The available series of lower molars of *Spalacolestes cretulablatta* encompasses a wide variety of wear stages. As wear progresses, the V-shaped notches in paracristid and protocristid become rounded and U-shaped. On m1, wear is heaviest on the protocristid, which develops a facet that dips distally. The wear facets on paracristid and protocristid are rather oblique to the occlusal plane in early wear, progressively becoming more parallel to that plane. In advanced wear stages (e.g., OMNH 27569, m6), the crown forms a continuous, concave, triangular wear surface that dips slightly in a mesial direction. Obliquely oriented striations are present on prevallid and postvallid faces of worn molars; these are more pronounced and recognizable on m4-6, where the mesial and distal faces of the teeth are somewhat more planar than on more anterior molars, where they are more convex. The rim of the cingulum forms a sharp ridge in unworn teeth, especially mesially and distally. With wear, small interstitial facets develop mesially and distally, and the sharp mesial and distal rims are beveled off into rather flat, obliquely oriented facets.

Mandible

Aside from small fragments, the dentary of *Spalacolestes cretulablatta* is known from two specimens, OMNH 29600 and 27421 (Figs 8, 9). OMNH 27421 preserves the horizontal ramus ventral to the level of m1, the posterior alveolus of m2, the base of m3, m4-5 intact, and paired alveoli for m6-7. Most of the ascending ramus and angular region are missing. OMNH 29600 (the holotype) includes the horizontal ramus posterior to m3 and preserves m4-7 in place. The crown of m4 is broken from its base and is rotated and displaced; minor postmortem rotation and displacement of the other molars has also occurred. The posterior and inferior margins of the angular region are intact, except for the loss of the condyle. The posterior margin is intact for a short distance dorsal to the position of the condyle; the coronoid process is broken obliquely and its full extent cannot be determined.

The horizontal ramus (Figs 8, 9) has a very gracile appearance compared to that of *Spalacotherium*. The ventral margin of the horizontal ramus appears somewhat bowed in lateral view, owing to a slightly greater depth beneath m4-5 than anteriorly or posteriorly. In dorsal view (Figs 8B, 9B), the ramus is relatively straight posterior to the level of m3; anterior to that tooth position, it curves medially. The ascending ramus arises about a molar's length posterior to the position of m7 and angles dorsally at about 45° with respect to the alveolar margin of the horizontal ramus. The posterior part of the jaw is also remarkably gracile in appearance, the bone being very thin in comparison to the far more robust (and larger) mandible of *Spalacotherium*. Proportionately, the ascending ramus is much longer anteroposteriorly than it is in *Spalacotherium*.

On the lateral side of the jaw (Figs 8C, 9C), the masseteric fossa is well marked and, owing to the form of the angular region (see below) and lateral flexure of the anterior margin of the ascending ramus, has the appearance of being quite deep. There is no labial mandibular foramen present at the apex of the masseteric fossa, as there is in a number of other primitive mammals (e.g., Dashzeveg & Kielan-Jaworowska 1984; Marshall & Kielan-Jaworowska 1992; Cifelli *et al.* 1998), although there is an extremely small nutritive foramen in one specimen (OMNH 29600) at a point somewhat dorsal to the apex of the masseteric fossa.

The anterior margins of the ascending ramus and masseteric fossa flex strongly in a lateral direction as they rise above the alveolar margin of the jaw. Similarly, the inferior margin of the dentary in the angular region has a salient lateral deflection. This strongly deflected angular region and lateral flexure of the anterior margin of the ascending ramus, together with similarly strong features on the lingual side of the mandible, give the dorsal

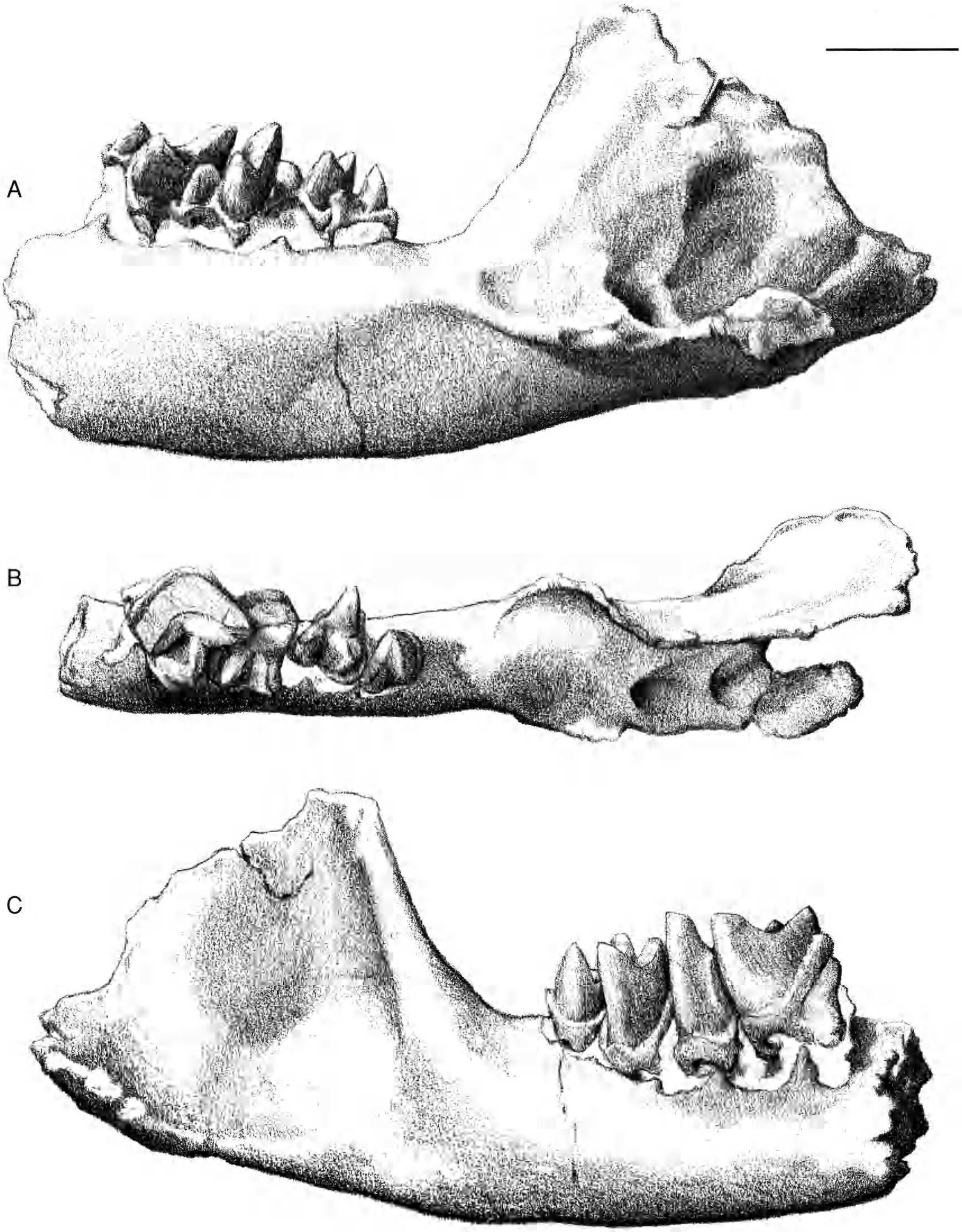

FIG. 8. — Dentary of *Spalacolestes cretulablatta* n. gen., n. sp. holotype (OMNH 29600), right dentary with m4-7, in lingual (**A**), occlusal (**B**), and labial (**C**) views. Scale bar: 2 mm.

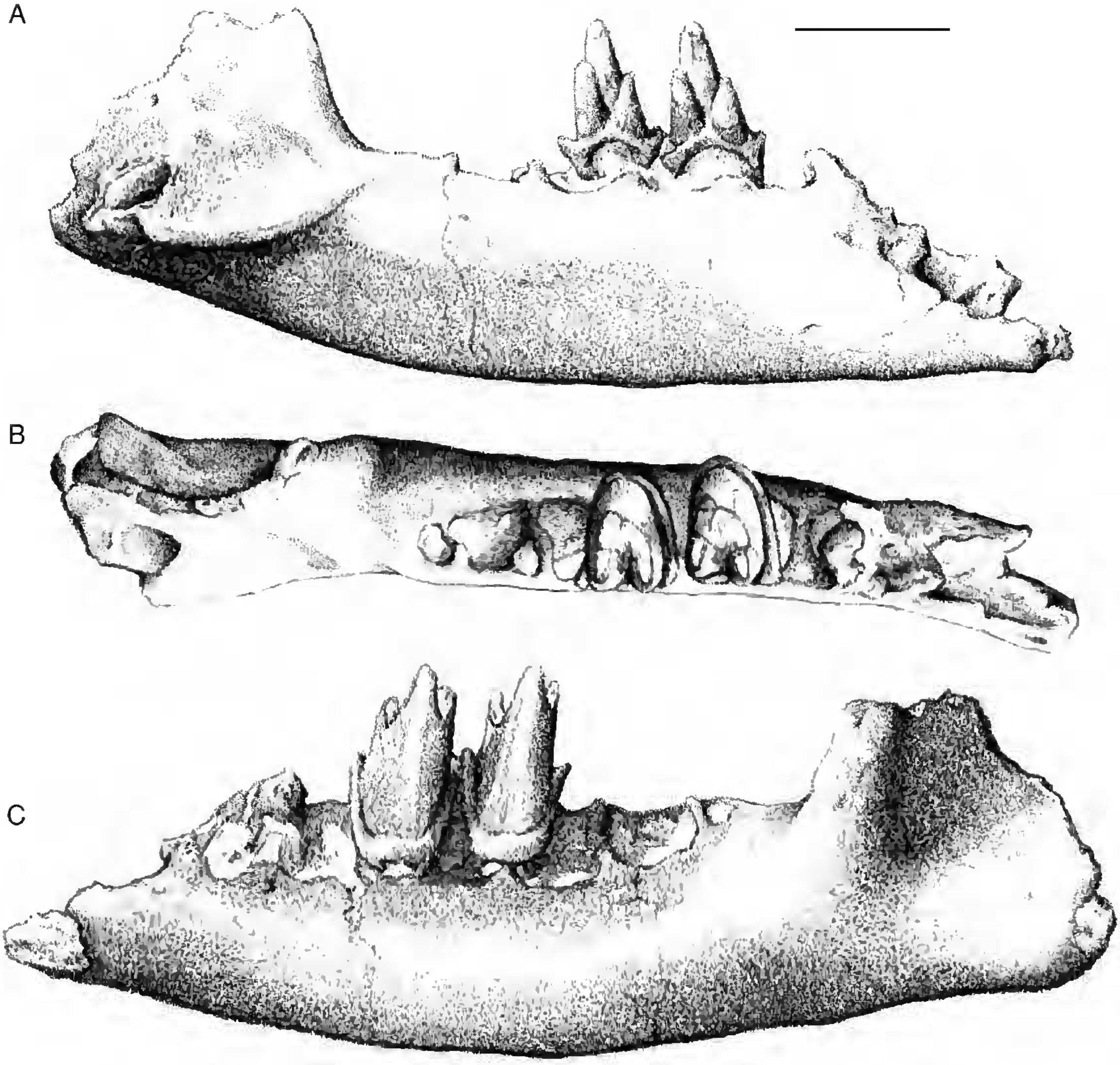

FIG. 9. — Dentary of *Spalacolestes cretulablatta* n. gen., n. sp. (OMNH 27421), left dentary with m4-5, in lingual (**A**), occlusal (**B**), and labial (**C**) views. Scale bar, 2 mm.

(Figs 8B, 9B) and posterior views of the mandible in *Spalacolestes cretulablatta* an appearance that is unique, so far as we are aware, among Mesozoic mammals.

On the lingual side of the jaw (Figs 8A, 9A), a strong crest, which we interpret as being for the insertion of the m. pterygoideus medialis, descends posteroinferiorly from the junction of the horizontal and ascending rami, beginning just below the alveolar margin. This crest strengthens to a shelf as it passes just inferior to the mandibular foramen, which has double openings for the mandibular canal on one specimen (Fig. 8B). The mandibular foramen is comparatively large and faces posterolabially, owing to the great development of the pterygoid crest beneath, the anterior and posterior margins of the mandibular foramen are developed as lips that project lingually as they descend to the pterygoid crest. A short distance posterior to the mandibular foramen, the pterygoid crest is developed as a salient process that thickens into a robust tip. A deep

TABLE 3. — Measurements (mm) and descriptive statistics for upper molars of *Spalacolestes cretulablatta* n. gen., n. sp. See Figure 2 for measurement definitions.

	M1	M2	M3	M4	M5	M6
L (N)	–	2	1	4	1	3
L (Range)	–	1.164-1.225	0.747	0.669-0.846	0.684	0.546-0.552
L (Mean)	–	1.195	0.747	0.745	0.684	0.549
L (CV)	–	0.036	1.000	0.103	1.000	0.006
ANW (N)	1	2	1	5	1	3
ANW (Range)	1.084	0.971-0.988	0.949	0.942-1.113	0.745	0.614-0.682
ANW (Mean)	1.084	0.979	0.949	1.034	0.745	0.656
ANW (CV)	1.000	0.012	1.000	0.065	1.000	0.056
POW (N)	–	3	2	5	1	3
POW (Range)	–	1.152-1.168	1.028-1.038	0.871-1.090	0.962	0.757-0.888
POW (Mean)	–	1.160	1.033	0.994	0.962	0.813
POW (CV)	–	0.007	0.007	0.107	1.000	0.083

pocket is enclosed between the pterygoid process (lingually) and the body of the dentary (labially). Where present, the pterygoid crest commonly extends posteriorly to the condylar region in Mesozoic mammals (e.g., Triconodontidae, Tinodontidae, Dryolestidae, see Simpson 1928a, 1929): in *Spalacolestes cretulablatta*, it terminates at the posterior margin of the process. The pterygoid fossa is very broadly developed anterior to the mandibular foramen, and in this respect differs from that of *Zhangheotherium*.

No meckelian groove or postdentary trough are apparent, nor are seats for the coronoid or other postdentary bones, as commonly seen in primitive mammals (Kermack & Mussett 1958; Kermack *et al.* 1968; Dashzeveg & Kielan-Jaworowska 1984; Kielan-Jaworowska & Dashzeveg 1989; Krebs 1991; Lillegraven & Krusat 1991; Nessov *et al.* 1994). A vestigial trace of the meckelian groove is present anteriorly on the dentary of *Zhangheotherium*, but a postdentary trough is lacking. The condyle is not preserved, but its position is shown by a slight thickening of bone just ventral to the preserved posterior margin of the ascending ramus in OMNH 29600 (Fig. 8A, C). The condyle would have been situated at, or slightly below, the alveolar margin of the horizontal ramus, lower than in *Spalacotherium* (e.g., BM 47750).

Upper molar series

The upper molars (Figs 10, 11) are two-rooted. They lack a lingual cingulum (although a faint basal swelling is variably present), as seen in *Symmetrodontoides canadensis* (see Fox 1985), and cusps on the pre- and postparacrista, as seen on upper molars of *Spalacotherium* (see Simpson 1928a), *Spalacotheroides* (see Patterson 1956), and *Zhangheotherium* (see Hu *et al.* 1997). Acuteness, transverse width, and height of the preparacrista relative to the postparacrista increase from M1 to M4, which is almost completely symmetrical. The parastylar lobe and distal stylar cusp are prominent on anterior molars (as they are in *Symmetrodontoides*), and decrease throughout the series. By contrast, the parastylar lobe is more strongly developed on posterior upper molars of *Spalacotherium* (see, e.g., Clemens 1963). The paracone is most distally recumbent on M1, decreasing in recumbency through M4, where it is symmetrical and erect. Past M4, molars are progressively smaller (Table 3), narrower labiolingually, and have a more posteriorly placed paracone. A composite restoration is shown in Figure 11; many of the trends evident in the restored series are also seen in the composite of *Kuehneotherium* (see Mills 1984).

The distolabial part of M1 (Fig. 10A, B) is not preserved on available specimens. The paracone is strongly recumbent distally; its mesial face is rounded, lacking the "pinched" appearance, with relatively straight shearing surface, of more distal teeth. A weak ridge, which develops heavy wear on its occlusal surface, descends almost vertically from the apex of the paracone down its mesolabial surface; this is equivalent to the prepara-

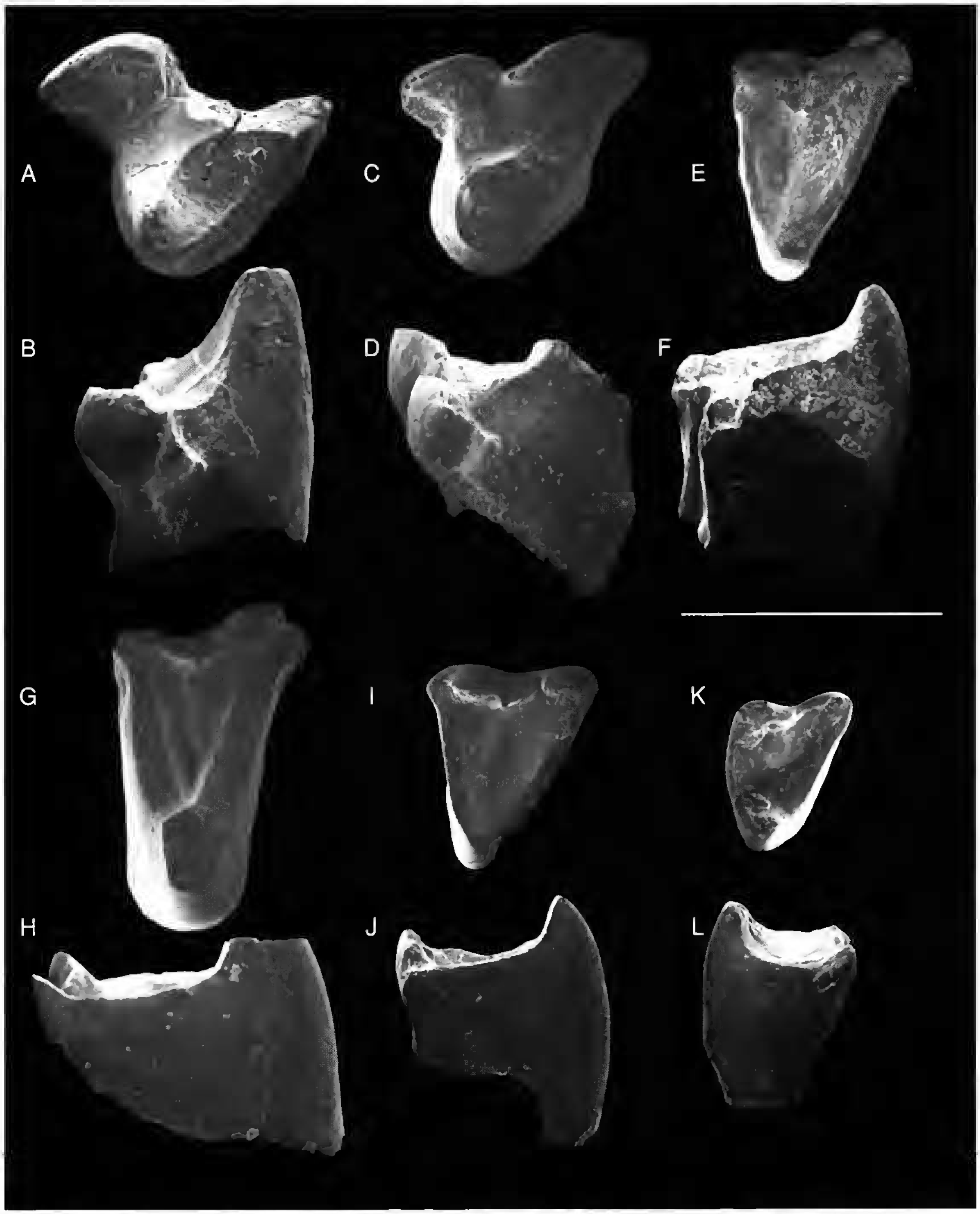

FIG. 10. — Scanning electron micrographs, upper molars of *Spalacolestes cretulablatta* n. gen., n. sp.; A, C, E, G, I, K, occlusal views; B, D, F, H, J, L, mesial views; **A, B**, left M1 (OMNH 26426); **C, D**, left M2 (OMNH 26686); **E, F**, left M3 (OMNH 33060); **G, H**, left M4 (OMNH 30611); **I, J**, left M5 (OMNH 25796); **K, L**, right M6 (OMNH 26691). Jaw fragments and roots eliminated where needed to improve clarity. Scale bar: 1 mm.

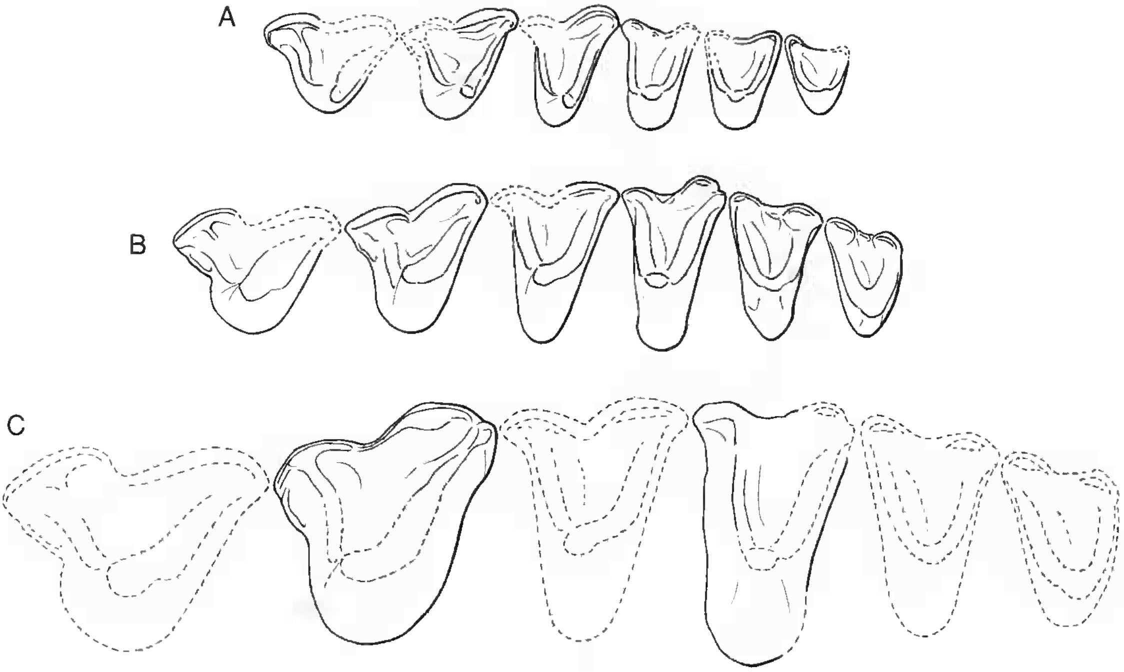

FIG. 11. — Composite upper molar series in occlusal view. **A**, *Spalacotheridium noblei* n. sp.; **B**, *Spalacolestes cretulablatta*, n. gen., n. sp.; **C**, *Spalacolestes inconcinnus*, n. gen., n. sp. Series scaled to relative size.

crista, but a crest as such is not developed until this surface approaches the parastyle, where its presence is only faintly suggested. The parastyle is very low, being placed near the base of the crown, and is developed as a prominent, mesially projecting lobe. A small accessory shelf descends lingually from the parastylar lobe near the labial terminus of the preparacrista, terminating at the base of the crown; there is no other hint of a cingulum, although the enamel is variably swollen on the lingual base of the tooth.

M2 (Fig. 10C, D) is generally similar to that of *Symmetrodontoides*, although the parastyle and metastyle are less developed. It differs from M1 in having a flattened mesial (prevallum) shearing surface, more strongly developed preparacrista, more acute angulation, less recumbency of the paracone, and less prominent, bulbous parastyle. The postparacrista descends at a steep angle from the apex of the paracone, forming a V-shaped notch near the base of that cusp. The crest terminates near the distolabial corner of the tooth, not quite reaching the small metastylar cusp. From the metastyle, a faint crest descends lingually for a short distance along the distal face of the tooth, terminating near the base of the tooth. This crest (perhaps a remnant of a cingulum) evidently formed the margin of the occlusal surface of the tooth, perhaps serving as a guide for the corresponding lower molar shearing surface: it is oriented at the same angle as wear striations located higher and more lingually on the same surface of the molar (e.g., OMNH 32897; Fig. 10C, D). Mesial to and separate from the metastylar cusp is a prominent, mesiodistally elongate, trenchant stylar cusp, as seen in *Symmetrodontoides*. This crestlike cusp extends mesially to the ectoflexus, where it meets a lower crest descending distally from the region of the stylocone. The latter cusp is not preserved on available specimens but, if present, it was small. None of the M3s in the sample is complete, but available specimens show a continuation of trends established in the upper molar series: the trigon is more acute and deeply basined; the paracone has only slight recumbency; the preparacrista is relatively higher; and the stylar cusp is smaller. One broken specimen (OMNH 33060; Fig. 10E, F) preserves the paraconal crests in pristine condition; cuspules are lacking from these.

M4 (Fig. 10G, H) is the most transversely developed, acute-angled, nearly symmetrical tooth of the series: in *Spalacotherium* (including *Peralestes*), it is M3 that appears to be most nearly symmetrical (Butler 1939). The paracone is mesiodistally compressed, with a distinct lingual fold, and is not recumbent. All specimens are almost perfectly symmetrical, except for minor differences in the parastylar and metastylar regions. The pre- and postparacristae are equal in height, enclosing a rather deep trigon basin, with flat, strap-like facets (as described for *Symmetrodontoides*, see Fox 1976, 1985) on their occlusal surfaces. The labial surface of the tooth bulges adjacent to the labial terminus of the preparacrista, suggesting the presence of a small stylocone (obliterated by wear on available specimens). Mesial to this, the parastyle is much reduced, forming an inconspicuous knob at the mesiolabial corner of the tooth. The metastyle is similarly developed; just mesial to it, the mesiodistally elongate stylar cusp is present along the margin of the stylar shelf. This stylar cusp is variable in development, being largest in the figured specimen (OMNH 30611; Fig. 10G, H), but is much reduced in comparison to more anterior molars. The cusp descends mesially as a crest rimming the stylar shelf and enclosing the trigon basin labially in the region of the ectoflexus, where there is variably (OMNH 26693, 30611) a small cuspule present.

M5 (Fig. 10I, J) is less transverse and forms a more obtuse angle than M4. It is somewhat lower crowned as well, although the pre- and postparacristae are high relative to the apex of the paracone, and enclose a deep trigon basin. The paracone is more distally placed than on M4 or preceding molars, recalling the condition in tribosphenic therians, where the protocone is more distally placed on distal molars. The trend in the molar series toward reduction of the parastyle is complete: no trace of it remains. There is a faint trace of the metastyle at the distolabial corner of the tooth. The distal margin of the stylar shelf is formed by the stylar cusp, which has twinned apices in the single complete specimen (OMNH 25796; Fig. 10I, J). This specimen is virtually unworn, and shows (again) the lack of accessory cusps on the pre- and postparacrista. It also shows that the stylocone, worn away in most other specimens available, is present and is developed as a trenchant, mesially placed counterpart to the distal stylar cusp.

M6 (Fig. 10K, L) is smaller and less transverse than M5. Parastyle and metastyle are lacking, and the labial part of the tooth is instead occupied by the stylocone and the distal stylar cusp, the latter not quite extending to the distolabial corner of the tooth. The paracone is more posteriorly placed than on M5; the distal face of the tooth is distinctive in being curved, with a rounded distolabial corner that differs from the more angular appearance of preceding molars.

Spalacolestes inconcinnus n. sp.

(Figs 6, 11-13)

HOLOTYPE. — Right m4, OMNH 33903.

HYPODIGM. — The holotype, and **m1**, OMNH 33039; **m3**, 33897; **M2**, 33034; **M4**, 33911.

LOCALITY AND HORIZON. — OMNH locality V868; upper part of Cedar Mountain Formation; Albian-Cenomanian.

ETYMOLOGY. — *Inconcinnus* (Latin), awkward, coarse, in reference to the appearance of the teeth when compared to the dainty, elegant morphology generally characterizing smaller species of Spalacotheriidae.

DIAGNOSIS. — The larger of the two species referred to the genus; lower molar cingulum better developed mesiolabially on m1 than in *Spalacolestes cretulablatta*, from which it also differs in having the trigon basin incompletely enclosed at the ectoflexus of posterior upper molars. Larger than *Symmetrodontoides foxi*; approximately similar in size to *S. canadensis*, from which it differs in having proportionately narrower lower molars and other generic characteristics.

DESCRIPTION AND COMMENTS

Teeth of *S. inconcinnus* n. sp. resemble those of

TABLE 4. — Measurements (mm) of *Spalacolestes inconcinnus* n. gen., n. sp.; see Figure 2 for measurement abbreviations and conventions.

Tooth	L	ANW	POW	Pad-med	Prd-med	Angle
m1	–	1.248	–	–	–	–
m3	0.962	1.270	–	0.667	0.739	43.097
m4	1.050	1.314	–	0.660	0.877	39.444
M2	1.861	1.356	1.601	–	–	–
M4	1.033	1.608	1.564	–	–	–

S. cretulablatta in most characteristics, differing chiefly in their much greater size (Fig. 4) and in features probably related to size (such as cusp robusticity). *S. inconcinnus* is much less common than either *S. cretulablatta* or *Spalacotheridium noblei* n. sp., being represented by only five molars, two from the upper dentition and three from the lower.

The lower molars are so similar to those of *S. cretulablatta* that only a few comments are warranted. The cingulum is more strongly developed than in *S. cretulablatta*, particularly on m1 (Fig. 12A, B). In addition, it appears that, in *S. inconcinnus*, the paraconid is lower relative to the metaconid at corresponding tooth positions. Variability cannot be assessed with the sample in hand, however, and this possible difference has accordingly been omitted from the diagnosis.

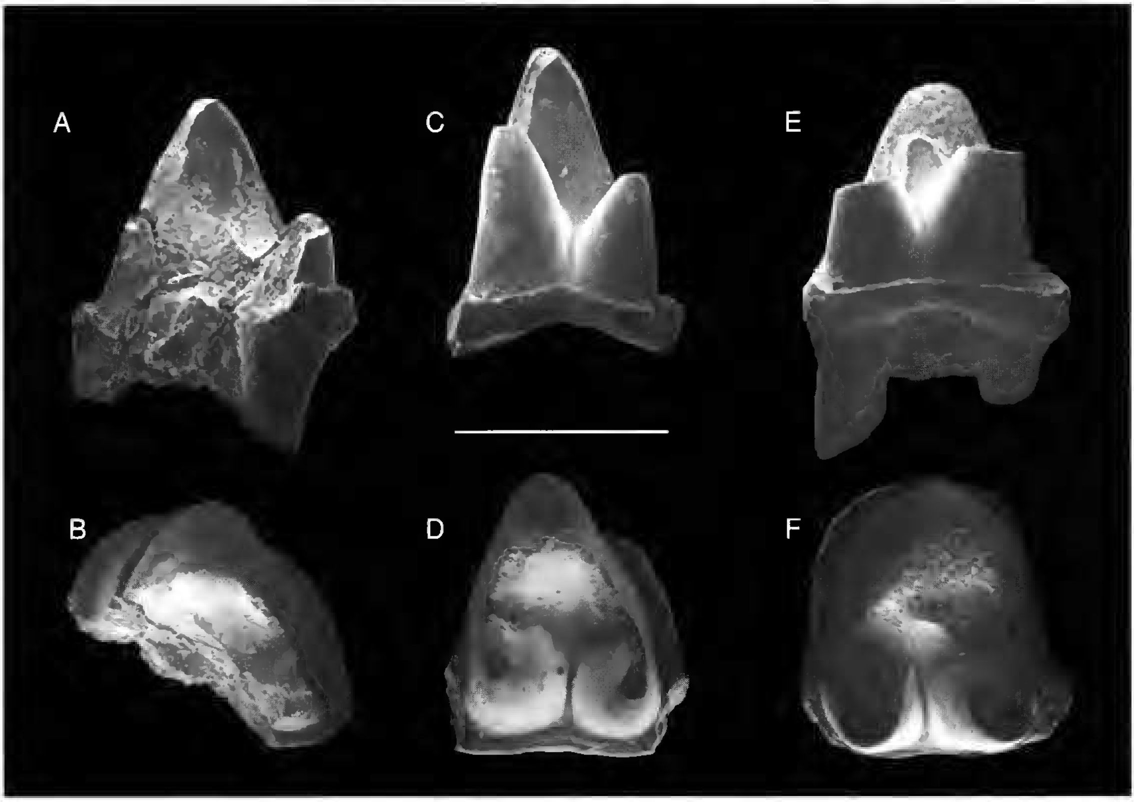

FIG. 12. — Scanning electron micrographs, lower molars of *Spalacolestes inconcinnus* n. gen., n. sp.; A, C, E, lingual views; B, D, F, occlusal views; **A**, **B**, right m1 (OMNH 33039); **C**, **D**, left m3 (OMNH 33897); **E**, **F**, right m4 (holotype, OMNH 33903). Scale bar: 1 mm.

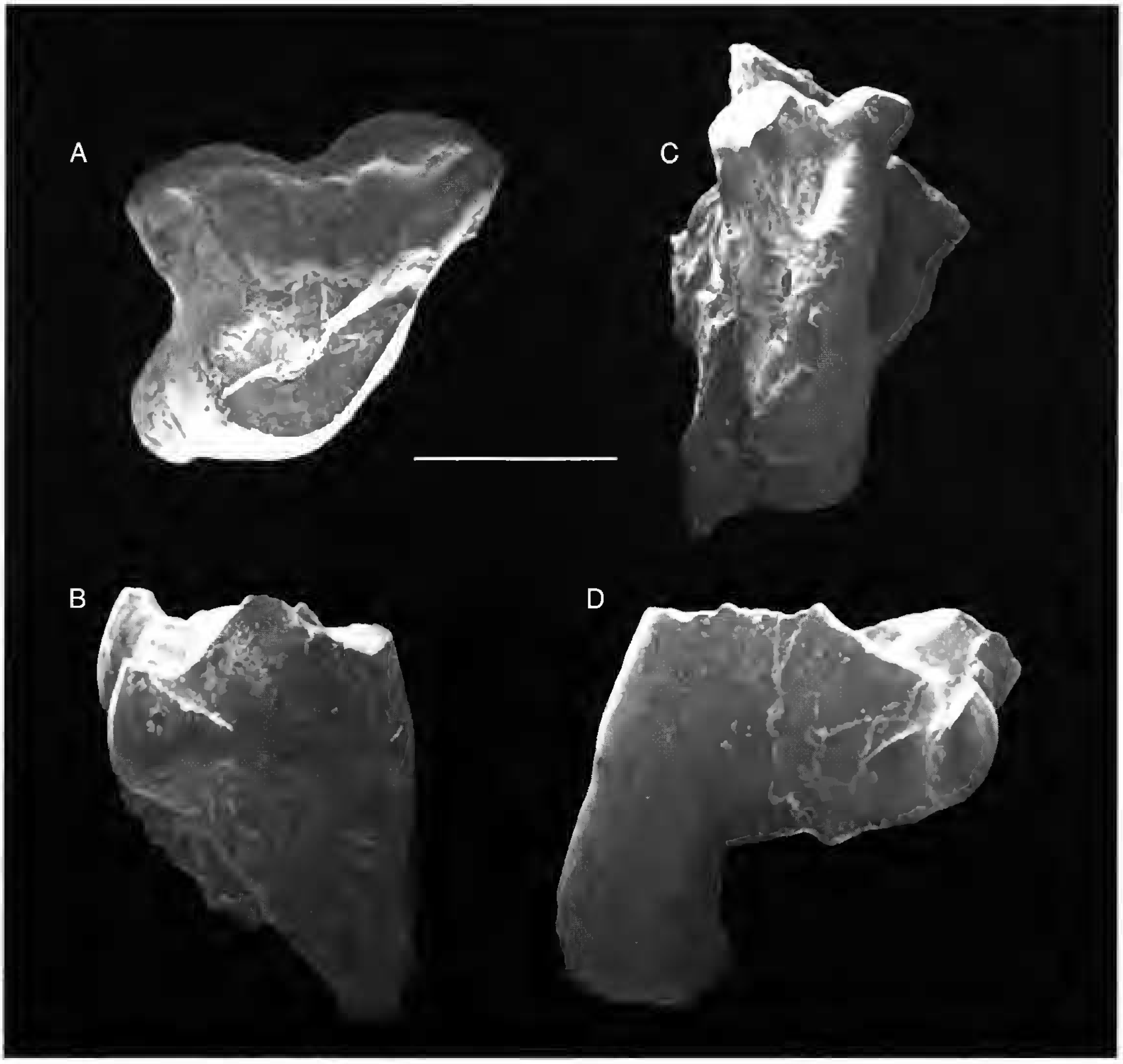

FIG. 13. — Scanning electron micrographs, upper molars of *Spalacolestes inconcinnus* n. gen., n. sp.; A, C, occlusal views; B, D, mesial views; **A**, **B**, left M2 (OMNH 33034); **C**, **D**, right M4 (OMNH 33911). Scale bar: 1 mm.

The only upper molar of *S. inconcinnus* in which the roots can be seen is OMNH 33034 (M2; Fig. 13A, B), where two are present. A faint swelling on the postparacrista, about two-thirds of the distance from paracone to metastyle, suggests the possible presence of a cusp on this crest, but breakage in this region precludes judgment on this point. The crest descending lingually from the metastyle on M2 is stronger but shorter than it is in *S. cretulablatta*. The distal stylar cusp is more bulbous, with a more pronounced labial bulge, than in *S. cretulablatta*; a weak crest, barely hinted at in the latter species, extends lingually into the trigon basin from the base of the stylar cusp. The presence of a small stylocone can be confirmed on M2 of *S. inconcinnus*. On M4 (Fig. 13C, D), the parastylar region and distal stylar cusp are more bulbous than in *S. cretulablatta*, so that the ectoflexus is deeper, although the distal stylar cusp of *S. cretulablatta* variably projects farther labially than in the single known M4 of *S. inconcinnus*. However, the crests descending to the ectoflexus from the stylocone and distal stylar cusp are very weak, so that the trigon basin is not enclosed labially, as it is in *S. cretulablatta*. OMNH 33911 includes the M4 embedded in a fragment of the maxilla. The labial margin of the tooth is oriented at a high angle with respect to the lateral side of the maxilla (the parastyle is near the lateral margin of the maxilla, whereas the distolabial corner of the tooth is some distance from it), suggesting that the rostrum flared laterally in this region (Fig. 13C).

Genus *Spalacotheridium* Cifelli, 1990

TYPE SPECIES. — *Spalacotheridium mckennai* Cifelli, 1990.

INCLUDED SPECIES. — The type, and *Spalacotheridium noblei* n. sp.

DISTRIBUTION. — Albian-Cenomanian through Turonian, Utah.

REVISED DIAGNOSIS. — Spalacotheriids differing from other members of the family in their small size (maximum length and width measurements of molars generally less than 0.75 mm). Lower molars differ from those of *Spalacotherium* in being more nearly symmetrical and acutely angled; from *Spalacotheroides* in having a complete labial cingulum; and from *Symmetrodontoides* and *Spalacolestes* in being lower crowned, with paraconid and metaconid subequal in development and of approximately equivalent height, only slightly lower than the protoconid, and in having posterior molars that are proportionately narrower and have more obtuse trigonid angles. Upper molars distinct from *Spalacotheroides* in the presence of a larger distally placed stylar cusp and more prominent parastylar hook (anterior loci), the lack of cusps B_1 and C, and the extremely low placement of the preparacrista (anterior loci). Upper molars differ from those of *Spalacolestes* in having a shallower trigon basin, and in the presence of a prominent parastyle on M6.

COMMENTS

This genus was originally based on a single molar of the type and then only species (Cifelli 1990). The recovery of another species, represented by a much more extensive sample from the Cedar Mountain Formation, upholds the morphological distinctiveness of these tiny symmetrodonts. Lower molars of *Spalacotheridium* are generally similar to *Spalacotheroides*, except for the described lack of a labial cingulum in the latter, but available materials of *Spalacotheroides* do not permit comparison between the two. In contrast, the upper molars of the two taxa are quite different. By comparison with *Spalacotherium*, *Spalacotheridium* appears to be primitive with respect to *Symmetrodontoides* and *Spalacolestes* in the features cited in the diagnosis.

Spalacotheridium noblei n. sp.
(Figs 6, 11, 14-16)

HOLOTYPE. — OMNH 25828, left m4.

HYPODIGM. — The holotype, and the following isolated teeth:
Lower molars: **m1**, OMNH 25609, 33038, 33205, 33221; **m2**, OMNH 30623, 33219; **m3**, OMNH 27261, 29605, 30630, 32948, 33041, 33229, 33900; **m4**, OMNH 25794, 26421, 27424, 27441, 27593, 29766, 30626, 30629, 32946, 33215, 33902; **m5**, 27258, 27629, 29607, 29653, 33052, 33053, 33224, 33899; **m6**, 29602.
Upper molars: **M1**, OMNH 26429; **M2**, OMNH 33061; **M3**, OMNH 30618, 33895; **M4**, OMNH 26689, 26692, 30617, 33232; **M5**, OMNH 27595, 33912; **M6**, OMNH 27461.

ADDITIONAL REFERRED SPECIMENS. — Incomplete upper molars, locus uncertain: OMNH 26687, 33236.

LOCALITIES AND HORIZON. — OMNH localities V235, V239, V240, V695, V696, V801, and V868; upper part of Cedar Mountain Formation; Albian-Cenomanian.

ETYMOLOGY. — For the Samuel Roberts Noble Foundation of Ardmore, Oklahoma, in recognition of its support for the Oklahoma Museum of Natural History.

DIAGNOSIS. — Differs from the most similar species, *S. mckennai*, in having smaller (especially in length) lower molars, with more acute trigonid angle on m4.

COMMENTS AND DESCRIPTION

S. noblei is rather similar to *S. mckennai* and is distinguishable because the sample of lower molars is sufficient to show that the few known specimens of the latter fall outside the range of size variation in *S. noblei*. The holotype of *S. mckennai* (MNA 5792), identified as m2, has

TABLE 5. — Descriptive statistics for lower molar measurements (mm) of *Spalacotheridium noblei* n. sp. See Figure 2 for measurement abbreviations and conventions.

	L	ANW	Pad-med	Prd-med	Angle
m1					
N	1	4	0	2	0
Range	0.888	0.692-0.722	–	0.532-0.626	–
Mean	0.888	0.710	–	0.579	–
CV	1.000	0.018	–	0.115	–
m2					
N	2	2	2	2	2
Range	0.447-0.482	0.475-0.601	0.359-0.398	0.396-0.441	49.781-54.643
Mean	0.465	0.538	0.379	0.418	52.212
CV	0.053	0.166	0.073	0.076	0.066
m3					
N	6	7	5	7	5
Range	0.421-0.539	0.633-0.795	0.340-0.411	0.416-0.511	42.789-47.581
Mean	0.490	0.711	0.393	0.460	45.490
CV	0.087	0.090	0.076	0.072	0.042
m4					
N	10	12	8	9	8
Range	0.411-0.559	0.559-0.745	0.318-0.389	0.402-0.562	33.018-41.155
Mean	0.485	0.678	0.358	0.490	38.105
CV	0.080	0.073	0.064	0.093	0.075
m5					
N	7	8	2	5	2
Range	0.409-0.465	0.608-0.720	0.348-0.360	0.424-0.492	37.875-39.004
Mean	0.446	0.671	0.354	0.452	38.439
CV	0.043	0.067	0.024	0.055	0.021
m6					
N	1	1	1	1	1
	0.352	0.537	0.270	0.400	36.642

length and width proportions similar to those of m3 in *S. noblei*, which is considerably larger, but the trigonid angle of MNA 5792 is much greater. When compared to m2 of *S. noblei*, on the other hand, MNA 5792 differs greatly in its proportions, falling near the maximum for width and the minimum for length (Tables 5, 6). All molars of *S. noblei* are shorter than m4 of *S. mckennai*, which has a relatively obtuse trigonid angle, despite its tooth position.

The lower molars of *Spalacotheridium noblei* differ from those of *Spalacolestes* and *Symmetrodontoides* in being proportionately lower crowned, with somewhat more obtuse trigonid angles at corresponding tooth positions. The most nearly complete m1 is OMNH 25609, which lacks only the tip of the metaconid and parts of the cingulum adjacent to that cusp (Fig. 14A, B). The paraconid appears to be relatively taller, with a broader, more robust base than is the case in *Symmetrodontoides* or *Spalacolestes*, although it is

TABLE 6. — Upper molar measurements (mm) of *Spalacotheridium noblei* n. sp. See Figure 2 for definition of measurements. Where more than one specimen was measureable a range is given: sample size for each appears in parentheses.

Tooth	L	ANW	POW
M1	–	1.175	–
M2	–	–	0.896
M3	0.646	0.743	0.917-0.957 (2)
M4	0.537-0.551 (3)	0.628-0.827 (2)	0.754-0.838 (3)
M5	0.649	0.795	0.746-0.838 (2)
M6	0.435	0.548	0.441

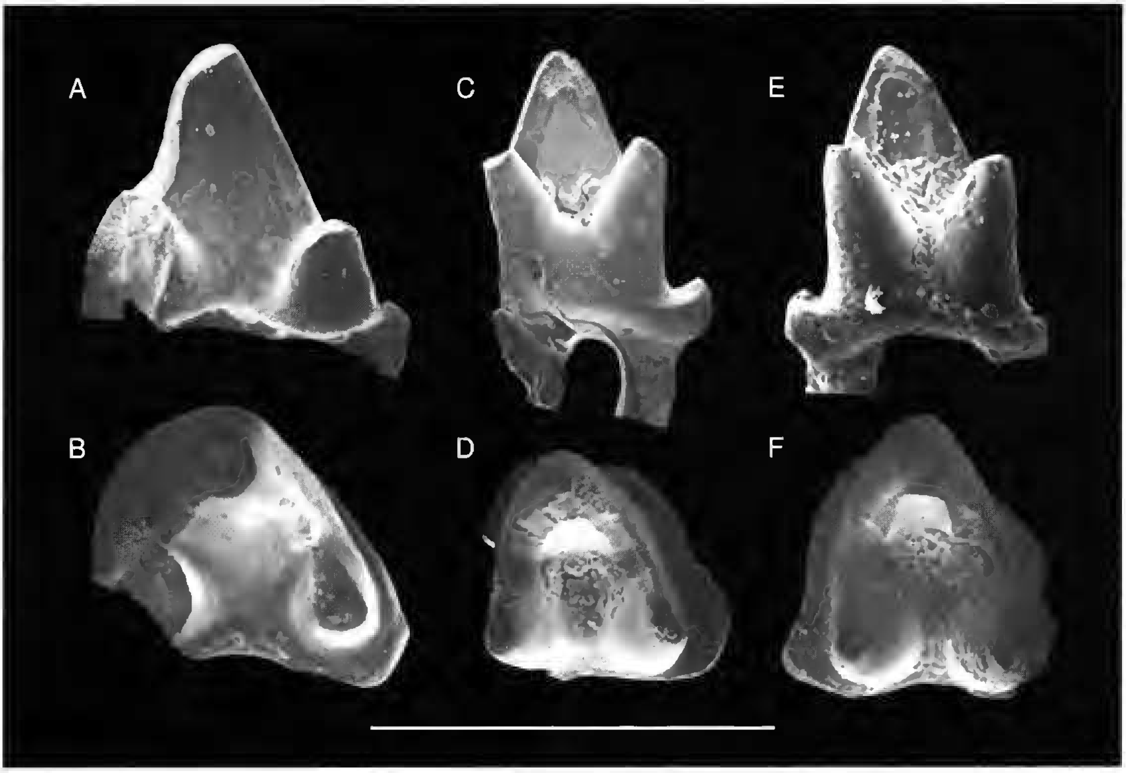

FIG. 14. — Scanning electron micrographs, anterior lower molars of *Spalacotheridium noblei* n. sp.; A, C, E, lingual views; B, D, F, occlusal views; **A**, **B**, left m1 (OMNH 26429); **C**, **D**, right m2 (OMNH 33219); **E**, **F**, left m4 (holotype, OMNH 25828). Scale bar: 1 mm.

still lower than the metaconid. As in all other North American Spalacotheriidae, m1 is morphologically distinctive by virtue of the anterior placement of the paraconid. Length to width proportions appear to change through the molars series about as in *Spalacolestes cretulablatta*, known by a much larger sample; the teeth are lower crowned than in *Symmetrodontoides* or *Spalacolestes*. The second molar (Fig. 14C, D) is considerably shorter than the first; absolute width increases through m4, with m5-6 being sequentially shorter and narrower than m4 (Table 5). On m2 and succeeding teeth, the paraconid is subequal to the metaconid and both cusps are taller relative to the protoconid than in *Spalacolestes* or *Symmetrodontoides*. However, the paracristid dips slightly lower in its median notch than does the protocristid. The cingulum is complete and, as in *Spalacolestes* and *Symmetrodontoides*, bears prominent cuspules at the mesio- and disto-lingual corners of the tooth. Also as in those taxa, the crown is much taller labially than lingually, and as a result, the cingulum descends noticeably as it proceeds labially from the interstitial regions of the tooth. On m4 (Fig. 14E, F), the metaconid is somewhat more lingually placed than the paraconid, so that the protocristid is slightly longer than the paracristid – a condition reminiscent of what is seen in *Symmetrodontoides*, although not so extreme, and the posterior molars never achieve the remarkable transverse expansion seen in that genus. The dental formula cannot be established with certainty. Identification of OMNH 29602 (Fig. 15C, D) as m6, however, seems probable because of its small size, low crown height, and proportions. This specimen appears to have an interstitial wear facet on the distal cingulum, suggesting the presence of a seventh molar; we tentatively regard the lower series to include seven molars.

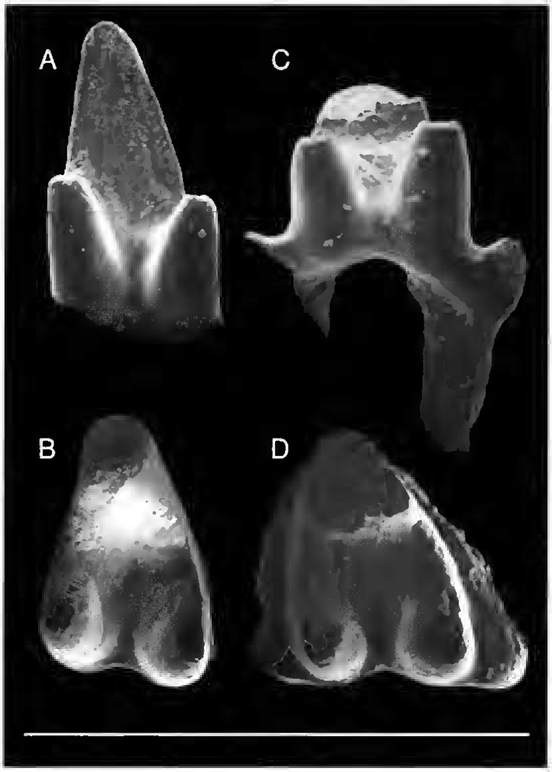

FIG. 15. — Scanning electron micrographs, posterior lower molars of *Spalacotheridium noblei* n. sp.; A, C, lingual views; B, D, occlusal views; **A**, **B**, left m5 (OMNH 27629); **C**, **D**, left m6 (OMNH 29602). Scale bar: 1 mm.

Wear on molar cusps and crests, prevallid and postvallid surfaces, and cingula is similar to that seen in *Symmetrodontoides* and *Spalacolestes* (see Fox 1976; Cifelli & Madsen 1986; and description above, see also Crompton *et al.* 1994 for discussion of the relationship between apical wear, shearing surfaces, and enamel microstructure). Strap-like facets develop along the dorsal surfaces of paracristid (where it develops earliest and most strongly; e.g., OMNH 27424) and protocristid, joining at the protoconid; as wear proceeds, these gradually form a triangular, concave facet with an emarginated base (corresponding to the notch between the bases of paraconid and metaconid). An unusual variant is OMNH 33899, a heavily worn m5 in which wear is stronger on the labial than lingual side of the tooth, with the result that the paraconid and metaconid are taller than the protoconid.

Upper molars (Figs 11, 16) are generally similar to those of *Spalacolestes cretulablatta* and will be described only where they differ or provide additional information. M1 (Fig. 16A, B) is slightly worn, but shows that the stylocone was little developed or absent. The parastylar shelf, which descends lingually from the mesolabial corner of the tooth, has a more planar surface than in *Spalacolestes cretulablatta.* This may be related to differing wear on the available specimens: the parastylar shelf bears a wear facet that is contiguous with the prevallum shearing surface, suggesting that the shelf may have served as a guide for the occluding lower molar. No complete or lightly worn specimens of M2-3 (Fig. 16C) are available; as far as can be determined, they show the progressive narrowing of the paracone and reduction of parastyle and metastyle seen in *S. cretulablatta* (Fig. 11); the metastyle appears to be less developed on corresponding teeth than in that species. The trigon basin is not nearly as deep as in *S. cretulablatta* or *Symmetrodontoides*; this is particularly noticeable on M4-5 (Fig. 16F-I), in which there is little relief on specimens that are only lightly worn (e.g., OMNH 26692, 27595). As with *Spalacolestes* and *Symmetrodontoides*, M4 is the most transversely developed of the upper molars, and is almost perfectly symmetrical. M6 (Fig. 16J) is impressive by virtue of its minuscule size, probably being smaller relative to M5 than in *Spalacolestes*. It is similar in having a curved distal surface and rounded metastylar region, but differs in being less transverse and in having a more prominent, projecting parastyle.

?Spalacotheriidae gen. & sp. indet.
(Fig. 17)

SPECIMENS. — Anterior lower molar, probably m2, OMNH 33896 (OMNH locality V868); posterior upper molar, perhaps M6, OMNH 29612 (OMNH locality V695).

COMMENTS AND DESCRIPTION

Two specimens (one upper molar and one lower molar) from the upper Cedar Mountain Formation cannot be referred to any of the three species described herein, and thus document the presence of at least one more species of non-

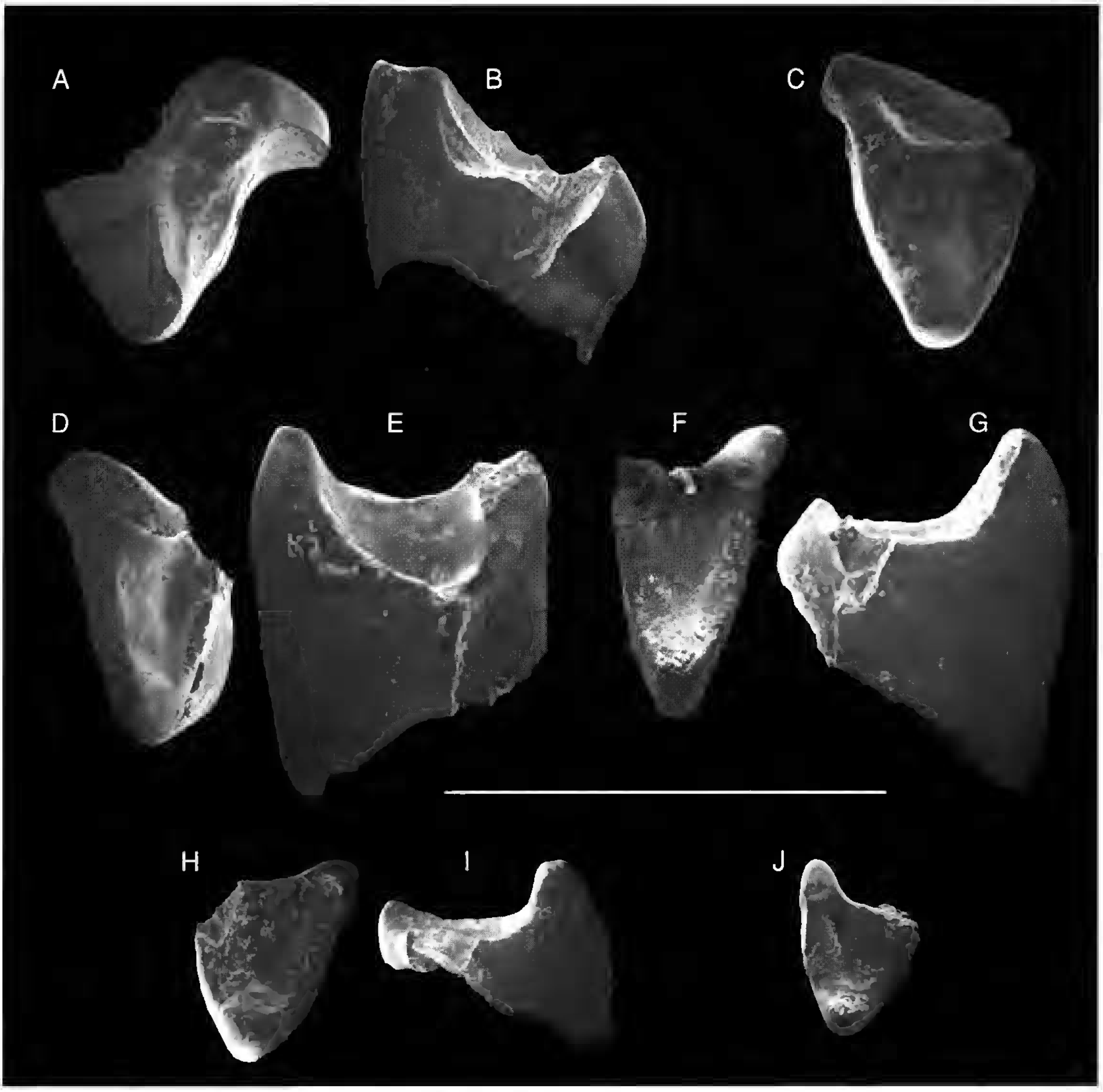

FIG. 16. — Scanning electron micrographs, upper molars of *Spalacotheridium noblei* n. sp.; A, C, D, F, H, J, occlusal views; B, E, G, I, mesial views; **A**, **B**, right M1 (OMNH 26429); **C**, right M2 (OMNH 33061); **D**, **E**, right M3 (OMNH 33895); **F**, **G**, left M4 (OMNH 26692); **H**, **I**, left M5 (OMNH 27595); **J**, left M6 (OMNH 27461). Scale bar: 1 mm.

tribosphenic Theria in the Mussentuchit local fauna. If locus is correctly interpreted, the teeth appear to come from animals of rather different size; hence, they cannot be referred to the same species based on present knowledge.

The lower molar (Fig. 17A, B), tentatively identified as m2, is intermediate between m1 and m2 of *Spalacolestes* or *Spalacotheridium* in terms of length-width proportions and general appearance: the paraconid is somewhat displaced anteriorly and in this respect is reminiscent of a spalacotheriid m1 (although it is not nearly so anteriorly placed as in m1 of all taxa known from the North American Cretaceous), yet this cusp is better developed, the crown is taller, and the trigonid angle more acute than is generally seen on that tooth. These features suggest that it is m2, implying that the specimen may represent a

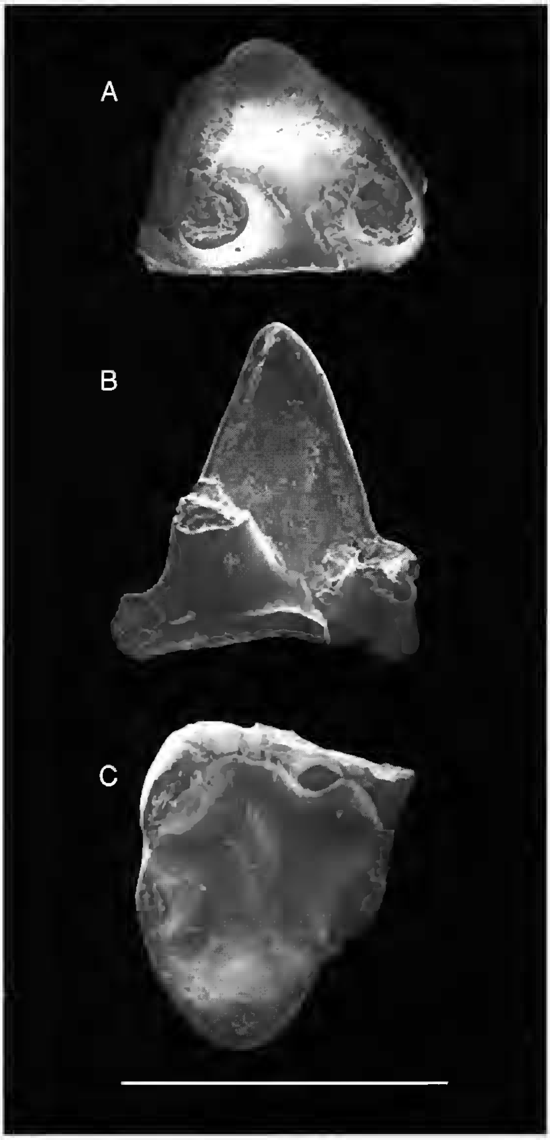

FIG. 17. — Spalacotheriidae gen. and sp. indet., **A**, **B**, left m2? (OMNH 33896) in occlusal (A) and lingual (B) views; **C**, right M6? (OMNH 29612) in occlusal view. Scale bar: 1 mm.

more primitive species than others known from the medial and Late Cretaceous of North America.

The upper molar (OMNH 29612; Fig. 17C) is strongly dissimilar to those of *Symmetrodontoides*, *Spalacotheridium*, and *Spalacolestes*. The absence of a metastylar projection, curvature of the postparacrista and rounding of the metastylar region, mesiodistal breadth and low height of the paracone relative to the rest of the crown, and possible projecting parastylar region (the tooth is broken), suggest that it represents a posterior locus, probably the last (M6, if the dental formula was as hypothesized for *Spalacolestes*). The metastylar cusp is prominent, and there is a second cusp (C) on the postparacrista, about midway between the paracone and the metastylar cusp, and separated from the latter by a slight notch. A weak crest extends into the trigon basin from the base of the paracone. The preparacrista is slightly lower than the postparacrista, and bears a cusp (B_1) that is somewhat closer to the stylocone (which is broken) than the paracone. Distal to the stylocone is a small but trenchant, mesiodistally elongate cusp that rims the labial margin of the trigon basin. A crest extending distally from this cusp does not quite reach the metastylar cusp, leaving the trigon basin open distolabially.

The presence of cusps B_1 and C on the pre- and postparacristae suggests that the upper molar (like the lower) represents a more primitive taxon than named species of Spalacotheriidae from the medial and Late Cretaceous of North America, and are resemblances to taxa such as *Spalacotheroides* (see Patterson 1956, fig. 1), *Zhangheotherium* (see Hu *et al.* 1997, fig. 2), and *Spalacotherium* (see Simpson 1928a, fig. 34); but it clearly differs from upper molars of these as well. Indeed, the presence of a crest extending labially from the paracone is a similarity to dryolestoids. Lacking any reasonable basis for comparison, we defer further comment on these puzzling specimens pending recovery of additional materials.

Genus *Symmetrodontoides* Fox, 1976

TYPE SPECIES. — *Symmetrodontoides canadensis* Fox, 1976.

INCLUDED SPECIES. — The type, *S. foxi* Cifelli & Madsen, 1986, and *S. oligodontos* Cifelli, 1990.

DISTRIBUTION. — Turonian through early Campanian, western North America.

REVISED DIAGNOSIS. — Large spalacotheriids differing from other members of the family in having proportionately broad, acutely-angled posterior lower molars (m4-6). Differs from *Spalacotheridium* in having lingually placed paraconid and height differential between paraconid and metaconid; differs from *Spalacolestes* in having more pronounced height differential between paraconid and metaconid; differs from both in having taller paraconid on m1, with taller paracristid. M1-2 differ from those of *Spalacolestes* and *Spalacotheridium* in having a paracone with less bulbous base and lingual face tightly arced or folded, not gently curving.

COMMENTS

Symmetrodontoides is not present in the Cedar Mountain Formation; its contents and diagnosis are included herein only to provide a basis for comparison. More extended diagnoses of *Symmetrodontoides* were given by Fox (1976, 1985), based on comparison with *Spalacotherium* and the single lower molar of *Spalacotheroides*. The discovery of additional taxa from the Cretaceous of North America shows that certain features cited in the earlier diagnoses of *Symmetrodontoides*, such as the presence of a labial cingulum and the progressive change in trigonid angle of the lower molars series, have a broader distribution than previously known.

DISCUSSION

Fragmentary as they are, new materials from the Cedar Mountain Formation of Utah add substantially to knowledge of symmetrodont diversity and morphology in the North American Cretaceous. Because many taxa are based on fragmentary, often non-comparable remains; because their teeth (upon which most taxa are based) are of rather simple construction; and because they remain poorly known in general, we do not believe that existing data are sufficient for synthetic consideration of symmetrodont phylogeny in the context of early mammal radiations. Accordingly, we restrict our treatment of relationships to discussion of character distributions and their possible implications for affinities of and within the Spalacotheriidae, summarizing these data in a traditional hypothesis of relationships within the family.

Sigogneau-Russell & Ensom (1998) have presented a detailed treatment of molar characteristics in Symmetrodonta (including many enigmatic taxa not treated herein), and we have relied on their work in compiling the following comparisons. These authors also point out that, in a number of respects, molars of spalacotheriid symmetrodonts are difficult to distinguish from those of certain dryolestoid eupantotheres; indeed, it is possible that dryolestoids are more closely related to spalacotheriids than has been generally believed (see, e.g., Sigogneau-Russell 1991a). In fulfilling our intent to focus on Spalacotheriidae, we cannot attempt comprehensive comparisons herein. We acknowledge the existence of a number of similarities in the molars of advanced spalacotheriids and certain dryolestids, such as the presence of a distal stylar cusp and a hooklike parastylar lobe, mesodistal compression of the crown, and other features cited by Sigogneau-Russell & Ensom (1998), as well as the markedly lower placement of lower molar labial cingulum than lingual cingulum. At the present state of knowledge, we believe that referral of the taxa considered herein from the North American Cretaceous (*Spalacotheroides*, *Symmetrodontoides*, *Spalacotheridium*, *Spalacolestes*) to Spalacotheriidae is more compelling than to Dryolestidae, based on features of the dentary (e.g., peculiar development of the pterygoid crest and masseteric flange) and lower dentition (e.g., extreme reduction of the talonid and characteristics of the roots, see Butler 1939). Based on size, morphological appropriateness and dissimilarity to other known elements of the Mussentuchit local fauna, and (especially) relative abundance and distribution among the known localities, we believe there is vanishingly little doubt as to the reference of upper and lower dentitions to the respective species described herein.

DENTARY

The structure of the dentary and associated postdentary bones has figured prominently in discussion of the origin and early differentiation of mammals (e.g., Crompton & Jenkins 1979; Kemp 1983). Mandibles ascribed to *Kuehneotherium* suggest that a full complement of attached postdentary bones was retained (Kermack *et al.* 1968), as they were in *Morganucodon* (see

Kermack *et al.* 1973), *Docodon* Marsh, 1881 (see Kermack & Mussett 1958), and *Haldanodon* Kühne & Krusat, 1972 (see Lillegraven & Krusat 1991). In these taxa, the posteromedial face of the dentary bears a prominent postdentary trough, overhung by a ridge, extending anteriorly from the condyle. The postdentary trough housed the articular, prearticular, surangular, and angular; attachment facets for the coronoid and splenial are generally also visible, more anteriorly on the dentary (e.g., Kermack *et al.* 1973, fig. 7; Lillegraven & Krusat 1991, fig. 14). The meckelian groove extends anteriorly from the mandibular foramen and is confluent with the postdentary trough; in *Morganucodon* it housed the anterior part of the prearticular (Kermack *et al.* 1973), whereas a splenial is associated with (or overlies part of) the meckelian groove in *Haldanodon* (see Lillegraven & Krusat 1991). Several other poorly understood or archaic mammals retain an essentially similar condition, although the trough and ridge are not as well developed (e.g., *Shuotherium* Chow & Rich, 1982; *Ausktribosphenos* Rich *et al.*, 1997). In most remaining mammals, the meckelian groove (where present) is separated from the mandibular foramen and the postdentary trough and corresponding ridge are lost, suggesting detachment of the main body of postdentary elements from the dentary, although attachment at their anterior extremity evidently persisted in some eupantotheres, such as *Amphitherium* Blainville, 1838 and *Peramus* Owen, 1871 (see Allin & Hopson 1992). The condition may be similar in the Late Jurassic or Early Cretaceous symmetrodont *Zhangheotherium*, which has a prominent meckelian groove and scars for the coronoid and splenial (Hu *et al.* 1997), and, possibly, another element in addition to the dentary (R. C. Fox, pers. comm.). A small coronoid apparently persisted in numerous mammalian groups. First reported among "pantotheres" by Krebs (1969), facets suggesting presence of the coronoid have been reported in the dryolestoid *Henkelotherium* Krebs, 1991 (see Krebs 1991), various triconodonts including *Phascolotherium* Owen, 1838 (BM 112) and *Gobiconodon* Trofimov, 1978 (see Jenkins & Schaff 1988), the eutherian *Prokennalestes* Kielan-Jaworowska & Dashzeveg, 1989 (see Kielan-Jaworowska & Dashzeveg 1989), paulchoffatiid multituberculates (Hahn 1977), and the spalacotheriid *Spalacotherium* (BM 47750). Persistence of the meckelian groove (or a remnant of it), which may have housed remnants of one or more postdentary elements, is even more widespread (see discussions in Bensley 1902; Simpson 1928b; Kermack *et al.* 1973). Among symmetrodonts, the meckelian groove is present in *Kuehneotherium* (see Kermack *et al.* 1968), *Tinodon* (see Simpson 1929), *Zhangheotherium* (see Hu *et al.* 1997), *Shuotherium* (see Chow & Rich 1982), and *Spalacotherium* (see Simpson 1928a). The presence and form of the meckelian groove have been used in interpreting the phylogeny of Mesozoic mammals (Luo 1994; see also Hu *et al.* 1998). Among the aforementioned taxa, the meckelian groove is reduced anteriorly in all; in *Zhangheotherium*, what remains is subparallel to the axis of the dentary, whereas in *Kuehneotherium*, *Tinodon*, *Spalacotherium*, *Tinodon*, and *Shuotherium* the meckelian groove converges toward the ventral margin of the dentary anteriorly. This latter state is presumed to be more derived (Luo 1994), but the significance of this distribution for symmetrodonts is unclear. Both the coronoid and meckelian groove are lacking in *Spalacolestes*, and available evidence suggests that the meckelian groove, at least, was lacking in *Symmetrodontoides*. Hence, both of these features were lost within Spalacotheriidae, assuming monophyly of the family.

In primitive mammals such as morganucodontids and *Kuehneotherium*, the ventral margin of the dentary is emarginated posteriorly (as it is in advanced cynodonts), where the postdentary elements are positioned (see, e.g., Kermack *et al.* 1968, 1973; Gambarayan & Kielan-Jaworowska 1995). The evolution of an angular region and process on the dentary of more derived mammals is uncertain because of disputed homologies and differing criteria on which recognition of these characters are based (see excellent discussion in Wible 1991). An anteriorly placed process is present in cynodonts (Sues 1986) and certain primitive mammals, such as *Morganucodon* (see Kermack *et al.* 1973), *Docodon* (see Kermack & Mussett 1958), and *Haldanodon* (see Lillegraven

& Krusat 1991). Rowe (1988) considered the loss of the anteriorly placed process as an advanced feature characterizing multituberculates and therians. Patterson (1956) disagreed with identification of this feature as a true angular process, pointing out the differences in both position and inferred function (see also Prothero 1981). In *Dinnetherium* Jenkins *et al.*, 1983 (see Jenkins *et al.* 1983), this anteriorly placed process occurs together with one that is more posteriorly placed, near the condyle, supporting Patterson (1956)'s suggestion that the former is not homologous with the angular process found among therian mammals (Jenkins *et al.* 1983; see also Crompton & Luo 1993). Sues (1986; see also Gambarayan & Kielan-Jaworowska 1995), however, suggested that the angular process of tritylodont therapsids and certain therians is homologous, indicating that the continuous ventral margin of the dentary as seen in taxa such as symmetrodonts could have been formed through fusion of the two processes seen in *Dinnetherium*. We can offer nothing in the way of new data to resolve this issue. It is worth pointing out, however, that all students who have commented on the matter have observed that symmetrodonts (e.g., *Kuehneotherium*, *Tinodon*, *Spalacotherium*, *Zhangheotherium*) lack an angular process or, for that matter, any ventral or posteroventral expansion of the dentary in the angular region (e.g., Simpson 1928a, 1929; Prothero 1981; Hu *et al.* 1997); an angular process is also lacking in triconodontids and gobiconodontids. This is distinctly different from the condition (where known) among eupantotheres and peramurans (e.g., *Amphitherium*, *Peramus*, Dryolestidae: see Prothero 1981) and among tribosphenic mammals. We tentatively recognize the development of a posteriorly placed angular process as a derived feature characterizing eupantotheres and tribosphenidans (Trechnotheria of Prothero 1981). This feature is absent in *Spalacolestes*, as it is in *Spalacotherium* and all other symmetrodonts.

A pterygoid crest or pterygoid shelf (Miao 1988; Rowe 1988; Gambarayan & Kielan-Jaworowska 1995) on the medial surface of the mandible may be related to increased importance of the pterygoid muscle in mandibular adduction, translation, and rotation (e.g., Oron & Crompton 1985). The pterygoid crest is lacking in primitive taxa such as *Morganucodon* (in which the medial pterygoid muscle is interpreted to have been small, Crompton & Hylander 1986) and *Kuehneotherium*. Prothero (1981) cited the presence of a pterygoid crest as a synapomorphy of Symmetrodonta (including Spalacotheriidae and Amphidontidae), but this crest enjoys a considerably broader distribution, being present in eupantotheres (e.g., *Laolestes* Simpson, 1927; *Amblotherium* Owen, 1871; see Simpson 1929: 63, 68), triconodontids (Simpson 1928b), gobiconodontids (Jenkins & Schaff 1988), multituberculates (Miao 1988; Gambarayan & Kielan-Jaworowska 1995), and tribosphenidans (Kielan-Jaworowska & Dashzeveg 1989, fig. 20; Sánchez-Villagra & Smith 1997), as well as symmetrodonts (except *Kuehneotherium*). Rowe (1988, 1993)'s Theriiomorpha includes a pterygoid shelf as a diagnostic character (see discussion in Miao 1993). Although the pterygoid crest (and its continuation onto the angle, where present, of the therian dentary) may be developed as a medial shelf (e.g., multituberculates, Marsh 1880; Gambarayan & Kielan-Jaworowska 1995) or inturned process (e.g., some Cretaceous Eutheria, Kielan-Jaworowska *et al.* 1979), the condition among marsupials (commonly termed an inflected angle) has been suggested to be a derived character unique to the group (Sánchez-Villagra & Smith 1997). However, using the definition these authors provide ["a medially inflected angular process may be defined as one that projects inward (lingually) at about 90 degrees with respect to the dorsoventral plane of the mandibular ramus," Sánchez-Villagra & Smith 1997: 120], we observe an inflected angle to be present in *Prokennalestes* (e.g., GI PST 10-5C, 10-6).

In *Spalacotherium*, the pterygoid crest originates just below the mandibular foramen. The crest is incompletely preserved in available specimens, so that its full extent cannot be determined. However, it was greatly expanded and, perhaps, developed a medial process in the region of the mandibular foramen, an unusual feature among early mammals. This clearly was the case with

Spalacolestes. Here the pterygoid crest begins just below the alveolar margin at the junction of horizontal and ascending rami, descending posteroventrally to the region of the mandibular foramen, where it is developed as a large, curving process that encloses a small pocket. The strong development of the pterygoid crest into a process near the mandibular foramen is unusual among early mammals; it is lacking in other symmetrodonts such as *Tinodon* and *Zhangheotherium.* The condition in *Spalacolestes*, in which there clearly is a large, reflected process and the pterygoid crest continues anterodorsally, is undoubtedly unusual and apomorphic. An edentulous dentary that we refer to *Spalacotheroides bridwelli* (FMNH PM 1025) preserves some limited information on the medial side of the jaw in this species. The pterygoid crest clearly originated just below the alveolar margin and extended posteroventrally, as in *Spalacolestes.* The specimen is considerably abraded in the vicinity of the mandibular foramen, and it is unclear whether the pterygoid crest was developed into a process, as in the taxon from Utah. To our knowledge, the only other Mesozoic mammal with a pterygoid crest that extends anterodorsally and nearly reaches the alveolar margin of the dentary is *Prokennalestes* (see Kielan-Jaworowska & Dashzeveg 1989, fig. 20).

A related and noteworthy feature on the medial side of the dentary in *Spalacolestes* is the great size of the pterygoid fossa (we are indebted to Z. Luo for suggesting this to us). In most Mesozoic mammals, such as triconodontids (see Simpson 1928a) and gobiconodontids (see Jenkins & Schaff 1988), the pterygoid fossa extends anteriorly to about the level of the mandibular foramen; in *Spalacolestes*, the pterygoid fossa extends well anterior to the mandibular foramen. Among spalacotheriids, the presumed primitive condition (pterygoid fossa terminates anteriorly adjacent to the mandibular foramen) is present in *Spalacotherium* (see Simpson 1928a) and *Zhangheotherium* (see Hu *et al.* 1997), whereas the pterygoid fossa extends farther anteriorly in *Spalacotheroides* (FMNH PM 1025). The posterior part of the dentary is not known in other taxa; nonetheless, this distribution suggests the possibility that the derived condition may represent a shared, derived feature of North American Spalacotheriidae.

The ventral margin of the dentary in the angular region of *Spalacotherium* is reflected laterally into a "wide, efflected, flange-like masseteric crest," as Simpson (1928a: 102) noted. The same is true, to a greater degree, in *Spalacolestes.* Although the posteroventral margin of the dentary has some lateral reflection in certain triconodonts (Hopson 1994) and gobiconodontids (Jenkins & Schaff 1988), it is not significantly developed in other symmetrodonts or other Mesozoic mammals, and the degree of reflection seen in *Spalacotherium* and (especially) *Spalacolestes* is unusual. The masseter muscle inserts along the ventral and lateral side of the dentary in this region, and the unusual condition in spalacotheriids is likely related to the development or configuration of this muscle (the masseteric fossa is also rather deep in *Spalacotherium* and *Spalacolestes*). Lacking the skull, functional interpretation is limited. However, the mandibular symphysis was probably unfused, as suggested by BM 47748, referred to *Spalacotherium.* The mandible of *Zhangheotherium* was also unfused (see Hu *et al.* 1997), as is the case with most early mammals (Crompton & Hylander 1986). It is likely that mastication in spalacotheriids involved significant components of mandibular rotation and lateral translation: the masseter serves to invert the dorsal border of the hemimandible on which it inserts, and the pterygoid serves to evert it (Oron & Crompton 1985; Crompton 1995). Hence, there is reason to believe that the unusual condition of the pterygoid crest and the lateral reflection of the posteroventral margin of the dentary in spalacotheriids are functionally related features, and that they may indicate some unusual aspect (perhaps strong development) of lateral translation or rotational movement in the masticatory cycle of these mammals, as suggested by consideration of their shearing surfaces (see also Patterson 1956: 57; Crompton 1971; Sigogneau-Russell & Ensom 1998). As has been described for lower molars of North American Spalacotheriidae (Fox 1976; Cifelli & Madsen 1986), upper molars of *Spalacotheridium* and *Spalacolestes* bear obliquely oriented wear striations on both prevallum and postvallum surfaces

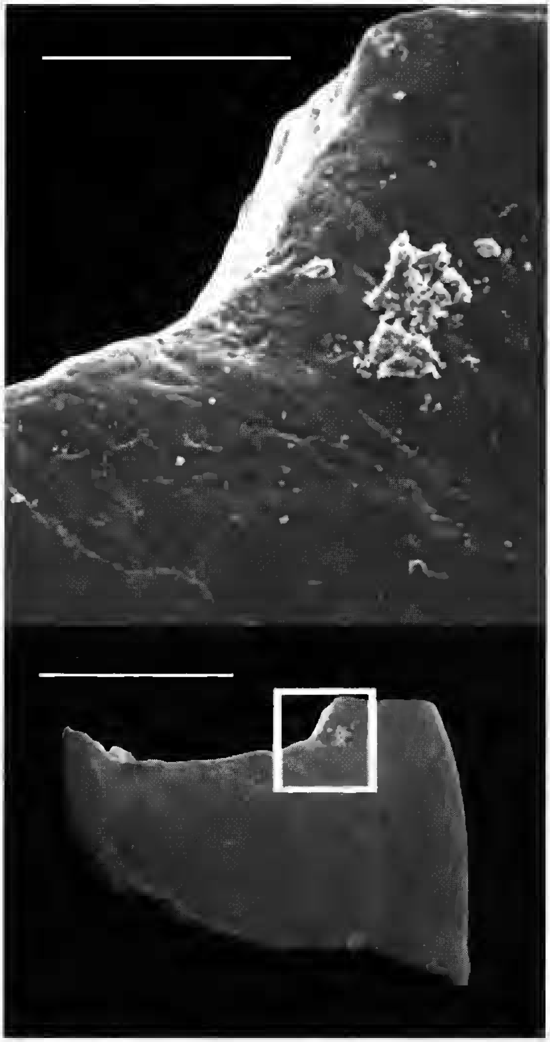

FIG. 18. — Microwear structures in *Spalacolestes cretulablatta* n. gen., n. sp.; bottom, mesial view showing prevallum shearing surface on left M4 (OMNH 30611); box indicates location of enlarged photo, above. Scale bars: top, 0.1 mm; bottom, 1 mm.

(Fig. 18). The relative contributions of lateral translation and rotation of the mandible in the masticatory cycle cannot be determined, although it is likely that both played significant roles.

LOWER MOLARS

We believe it highly probable that the lower tooth series of *Spalacolestes* (and, tentatively, *Spalacotheridium*) included seven molars, as in *Spalacotherium* (see Simpson 1928a; Clemens 1963); four are present in *Tinodon* (see Simpson 1929), six in *Zhangheotherium* (the described specimen is a juvenile and it is possible that not all molars were erupted, see Hu *et al.* 1997), and three to six in *Kuehneotherium*. Based on study of edentulous jaws, the lower part of this range was thought to be most probable for *Kuehneotherium* (see Kermack *et al.* 1968). Study of isolated teeth suggests that as many as six molars may have been present in some individuals (Mills 1984); the most complete alveolar row known for the genus shows that at least five were present on this specimen (Gill 1974). As noted by Patterson (1956), the molar count in symmetrodonts is correlated with angulation between principal cusps: "acute-angled" symmetrodonts are characterized by a high number of molars. On this basis, remaining taxa from the North American Cretaceous (*Spalacotheroides*, *Symmetrodontoides*) probably also had a high number of lower molars, seven being the likely number. Judged by comparison to *Kuehneotherium* and other outgroup taxa, the acute angulation and high molar count of spalacotheriids represents the derived condition.

Individual molar characteristics also set North American Cretaceous taxa and *Spalacotherium* apart from *Kuehneotherium*, *Tinodon*, and certain other symmetrodonts. In *Kuehneotherium* (and probably *Woutersia* as well), as in morganucodontids, precise occlusion is dependent on development of extensive wear facets on corresponding upper and lower molars. In spalacotheriids, however, matching molar surfaces fit more precisely (Crompton & Hylander 1986; Crompton 1995), as they do in tribosphenic therians. In *Tinodon*, as in *Kuehneotherium*, separate wear facets develop on occluding surfaces of the principal cusps, whereas in spalacotheriids, strong crests are developed between the protoconid and lingual cusps, and these form continuous prevallid and postvallid shearing surfaces (Crompton & Jenkins 1967; Crompton 1971). The condition in *Zhangheotherium* is uncertain, but it has been described as differing from other spalacotheriids in having rounded, conical cusps that lack connecting crests (Hu *et al.* 1997), strongly suggesting that it is similar to *Tinodon* or *Kuehneotherium* in lacking continuous shearing surfaces.

The cingulum and cingular cusps also are variable among symmetrodonts. In *Kuehneotherium* and *Tinodon*, only a lingual cingulum is present on the lower molars, the distolingual (talonid) cusp is moderately well developed, and two mesial cingular cusps are present (Crompton & Jenkins 1967). A cingulum is lacking from lower molars of *Zhangheotherium* (see Hu *et al.* 1997); it is incomplete labially, at least, in most other primitive mammals, such as *Woutersia* (see Sigogneau-Russell & Hahn 1995), *Morganucodon* (see Kermack *et al.* 1973), and Amphidontidae (see Simpson 1929; Trofimov 1980). In spalacotheriids, a single mesial cusp is present and the talonid is somewhat smaller than it is in *Tinodon* and *Kuehneotherium* (Crompton & Jenkins 1967). In addition, all spalacotheriids – with the exception of *Zhangheotherium* and the apparent exception of *Spalacotheroides* (see above) – have a complete labial cingulum on the lower molars. In all of these features, Spalacotheriidae appear to be derived with respect to remaining symmetrodonts (see Sigogneau-Russell & Ensom 1998 for discussion of the distribution and variability in the development of the lower molar cingulum among symmetrodonts).

Spalacotheriidae also appear to be unusual among Mesozoic mammals in the manner in which their lower molars interlock (we are grateful to Z. Luo for pointing this out to us). In morganucodontids and docodonts, the distalmost molar cusp, cusp d, fits between cusps b and e of the succeeding tooth (see, e.g., Crompton & Jenkins 1968); presumably modified arrangements are present in other taxa, such as *Kuehneotherium*, gobiconodontids, and triconodontids (see Luo 1994; Kielan-Jaworowska & Dashzeveg 1998). In spalacotheriids, the distal cingular cusp (which appears to be homologous with cusp d) is placed lingual to the mesial cingular cusp (which occupies a similar position to cusp e and may be homologous with it) of the following tooth, and the mesial cingular cusp fits into an embayment of the cingulum that is labial to cusp d of the preceding tooth.

Within Spalacotheriidae, taxa from the North American Cretaceous appear to be advanced with respect to *Spalacotherium* in having more acutely angled, higher crowned lower molar trigonids; *Spalacotheridium* is the least extreme in this regard (the condition is unclear in *Spalacotheroides*, but it is probably safe to say that its lower molars are more acutely angled than are those of *Spalacotherium*). In species of *Spalacolestes* and *Symmetrodontoides*, the paraconid and paracristid are distinctly lower than the metaconid and metacristid on all lower molars (except m7, which in *Spalacolestes* at least, lacks a metaconid); in species of *Symmetrodontoides*, the height differential is accentuated. The cusps are subequally developed in *Spalacotheridium*, *Spalacotherium* (see Simpson 1928a), and *Tinodon*, except on m1, where the paraconid is slightly smaller (e.g., USNM 2131). In *Woutersia* (see Sigogneau-Russell & Hahn 1995), by contrast, the paraconid is the taller of the two; in *Kuehneotherium* (see Kermack *et al.* 1968; Mills 1984), the condition is variable and the cusps should be considered subequal in development. We concur with Sigogneau-Russell & Ensom (1998) in believing that paraconid and metaconid were primitively subequal in Spalacotheriidae (as they are, for example, in *Zhangheotherium*), and conclude that the condition in *Spalacolestes* and *Symmetrodontoides* is derived. Both of the last-mentioned genera are characterized by the presence of posterior lower molars that are labiolingually expanded, owing to a relatively elongate paracristid and lingually placed paraconid.

Upper molars

As with the lower molars, the upper molars of Spalacotheriidae are more acute-angled than those of primitive taxa such as *Kuehneotherium* (see Kermack *et al.* 1968) and *Tinodon* (see Simpson 1929). Upper molars of *Spalacolestes*, *Symmetrodontoides*, and *Spalacotheridium*, at least, are more acute-angled (assumed to represent the derived condition) than those of *Spalacotherium* or *Zhangheotherium*. The single upper molar of *Spalacotheroides* illustrated by Patterson (1956, fig. 1) probably represents one of the mesial loci; other specimens (e.g., FMNH PM 1133, 1236) are distinctly more acute. *Microderson* (see Sigogneau-Russell 1991b), which resembles North American taxa in several other respects, is also rather acutely angled. The paracone on upper molars of *Spalacotherium* and *Zhangheotherium*, like that of North American Spalacotheriidae, is extremely tall relative to the condition seen in most outgroup taxa (e.g., *Tinodon*, *Kuehneotherium*). We suspect that paracone height will prove to be a useful character for or within Spalacotheriidae when its distribution becomes better known.

Recent studies (e.g., Hu *et al.* 1997; Sigogneau-Russell & Ensom 1998) have followed Patterson (1956) in identifying the mesiolabial cusp on upper molars of *Spalacotherium* (lacking at mesial loci, see Butler 1939) as the stylocone, or cusp B; hence, the more lingually placed cusp on the preparacrista is a neomorph by comparison to outgroup taxa such as *Kuehneotherium*. This cusp (termed B_1 by Hu *et al.* 1997) is also present in *Zhangheotherium* and *Spalacotheroides* (except the mesial molar, FMNH PM 1235, figured by Patterson 1956): is it primitive for Spalacotheriidae, or a derived feature characterizing these three genera? Other features, such as the presence of fewer than six upper molars and the ?lack of continuous shearing surfaces, suggest that *Zhangheotherium* represents the sister-taxon to remaining Spalacotheriidae, in turn providing some tentative evidence that the presence of this cusp may be primitive for the family. Under this interpretation, the absence of cusp B_1 in North American Spalacotheriidae (except *Spalacotheroides*) would represent a loss. Patterson (1956) also suggested that the mesialmost stylar cusp of *Spalacotheroides*, which lies mesial to the preparacrista, is a new cusp not present in *Spalacotherium*, and that it represents one of several, independent acquisitions of a parastylar cusp in therian mammals. Interpretation of this feature is problematic. A parastylar cusp is lacking in *Zhangheotherium* (see Hu *et al.* 1997). The single known upper molar of *Tinodon* (YPM 13637) lacks the parastylar region of the tooth, although Crompton (1971) restored *Tinodon* with a parastylar cusp. A cusp in this position is present in *Kuehneotherium* (see Kermack *et al.* 1968). Regardless, the prominent, hooklike parastylar region seen on anterior molars of *Symmetrodontoides* (see Fox 1985), *Spalacotheridium*, and *Spalacolestes* would appear to be an advanced condition by comparison to remaining taxa (see Sigogneau-Russell & Ensom 1998). Of the remaining upper molar cusps, cusp C is well marked in outgroup taxa such as *Kuehneotherium* and *Tinodon*, and is present in *Zhangheotherium*, *Spalacotherium*, *Microderson*, and *Spalacotheroides*. This suggests that the absence of cusp C in taxa from the medial and Late Cretaceous of North America represents an advanced condition. As described by Patterson (1956), *Spalacotheroides* has two distolabially placed stylar cusps (a metastyle and one that is more mesially placed at the margin of the stylar shelf), whereas only one is present in *Spalacotherium* (see Clemens 1963: 376). A single distolabial cusp (metastyle) is seen in *Kuehneotherium* (see Kermack *et al.* 1968), *Microderson* (see Sigogneau-Russell 1991b), and *Zhangheotherium* (cusp "D" of Hu *et al.* 1997). Positional evidence favors homology of the distalmost cusp (metastyle; see above) on upper molars of these taxa, suggesting that the more mesial cusp of *Spalacotheroides* is a neomorph. Taxa from the medial and Late Cretaceous of North America have the distolabially placed metastylar cusp and, more mesially, a mesiodistally expanded cusp at the margin of the stylar shelf. We tentatively regard the latter as homologous with the mesial of the two distal stylar cusps in *Spalacotheroides* (which we interpret to be stylar cusp "D" of Sigogneau-Russell & Ensom 1998), and its presence as an advanced feature characterizing North American Spalacotheriidae. The condition in *Spalacolestes*, *Spalacotheridium*, and *Symmetrodontoides*, in which the mesial of the two cusps is strongly developed on mesial molars, represents a more derived condition. A strongly developed distal stylar cusp is also present in the enigmatic *Thereuodon* from the Early Cretaceous of Morocco and England, which is otherwise so different as to be non-comparable (see Sigogneau-Russell 1989; Sigogneau-Russell & Ensom 1998).

In *Spalacotheroides*, as in remaining North American Spalacotheriidae, the preparacrista is markedly lower than the postparacrista, particularly on mesial molars. Judged by comparison with *Tinodon* and *Kuehneotherium*, this appears to be a derived condition, but the distribution of the character is difficult to determine from available literature. The preparacrista is clearly lower than the postparacrista in *Microderson*, whereas the crests appear to be subequal in development in *Spalacotherium* (see Simpson 1928a, fig. 34) and *Zhangheotherium* (see Hu *et al.* 1997, fig. 2). As noted by Fox (1985), the stylocone is so small in *Symmetrodontoides* that it is indistinguishable in teeth that have been subject to even moderate wear. The stylocone is also small in *Spalacolestes* and *Spalacotheridium*. Comparison with remaining Spalacotheriidae (*Spalacotherium*, *Spalacotheroides*, *Zhangheotherium*), as well as *Kuehneotherium*, *Woutersia*, and *Tinodon* (in which the stylocone is prominent), indicates that the stylocone has probably undergone reduction in the taxa from the medial and Late Cretaceous of North America (see also Sigogneau-Russell & Ensom 1998).

Comparison of upper molar shape and proportions in Spalacotheriidae is problematic because series are known for so few taxa and because, as shown above, coronal profile and degree of symmetry varies according to tooth position. M1/1 of *Spalacotherium* is considerably smaller than succeeding molars, whereas in *Spalacotheridium* and *Spalacolestes*, M1/1 is relatively much larger (e.g., Figs 6, 11, compare with Butler 1939, fig. 7). Insufficient basis for comparison leaves us uncertain as to the significance and polarity of this feature. *Spalacotheridium*, *Symmetrodontoides*, and *Spalacolestes* have an M4 that is remarkably symmetrical. Past this tooth position, molar size decreases, and the last molar is significantly smaller than its predecessor. Comparison to *Spalacotherium* suggests that these may be advanced conditions. In *Spalacotherium*, posterior molars sequentially develop a parastylar lobe that, on the last tooth, projects strongly. A small parastylar lobe is present on posterior molars of *Spalacotheridium* but lacking in *Spalacolestes* and *Symmetrodontoides*, suggesting reduction in the latter two taxa. All three North American genera differ from *Spalacotherium* in having the paracone progressively placed more distally on posterior molars (vaguely recalling a similar shift in the protocone of posterior upper molars in tribosphenic mammals). In terms of crown relief, *Spalacolestes* and *Symmetrodontoides* differ from *Spalacotheridium* in having a relatively deeper trigon basin. *Microderson* also appears to have a deep trigon basin, but this appearance is due to the fact that the paracone is extremely tall in this taxon. In remaining Spalacotheriidae, the trigon is much shallower than in *Spalacolestes* and *Symmetrodontoides*, so we interpret a shallow trigon basis as most probably representing the primitive condition.

Relationships and concluding remarks

To summarize, the limited data in hand suggest that recently described *Zhangheotherium* is primitive in several respects, and represents the sister-taxon to remaining Spalacotheriidae (Fig. 19). *Spalacotherium*, in turn, evidently is the sister-taxon to North American Spalacotheriidae. (We have omitted *Microderson*, known by a single upper molar, from our phylogeny. As noted above, this Moroccan taxon resembles one or another of the North American spalacotheriids in several respects, but the significance of these resemblances cannot be evaluated with data in hand; see discussion in Sigogneau-Russell 1991b.) Of the North American spalacotheriids, the geologically oldest, *Spalacotheroides bridwelli* from the Aptian-Albian, appears to retain the most number of primitive features, such as the presence of cusps B_1 and C on the upper molars (assuming that the presence of these cusps is primitive for Spalacotheriidae). *S. bridwelli* is unusual within the family in that the labial cingulum of lower molars is apparently incomplete (see Fox 1976). If this condition is correctly interpreted and not simply a matter of preservation (the holotype, FMNH PM 933, includes the only known lower molar of this species, and it may be abraded), then we believe *S. bridwelli* to be autapomorphic in this respect. Of remaining genera, neither *Spalacotheridium* nor *Spalacolestes* (two species each) is characterized by known synapomorphies, unless the slight elongation of the paracristid on lower molars of *Spalacolestes cretulablatta* and *S. inconcinnus* represents a shared derived character. *Symmetrodontoides* (three species) is the geologically youngest and most advanced member of the family, characterized by labiolingually expanded posterior lower molars.

Some members of the Mussentuchit local fauna,

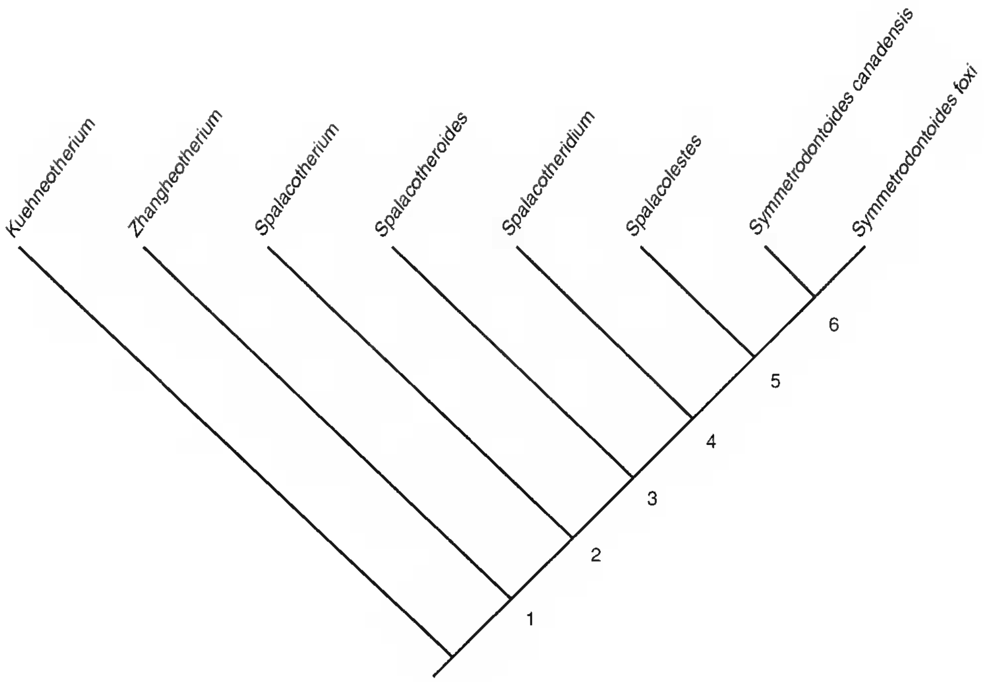

FIG. 19. — Hypothesis of relationships among Spalacotheriidae; *Kuehneotherium* included as outgroup, *Microderson* omitted because of insufficient data; additional North American species (*Symmetrodontoides oligodontos*, *Spalacotheridium mckennai*, *Spalacolestes inconcinnus*) not included because they are poorly known and, based on present knowledge, add no detail to the phylogeny presented. Characters at nodes (see discussion in text): **1**, (Spalacotheriidae) molars acutely angled; ?gain extra cusp (B1 of Hu *et al.* 1997) on upper molars; single mesial cingular cusp on lower molars; reduce distal cingular cusp (talonid) on lower molars; unique lower molar interlocking mechanism, whereby the distal cingular cusp of one molar is placed labial to the mesial cingular cusp of the succeeding tooth; **2**, six or more upper and lower molars present; ?pterygoid crest strongly developed in region of mandibular foramen (known only for *Spalacotherium* and *Spalacolestes*); continuous prevallum and postvallum shearing surfaces on molars; ?posteroinferior border of dentary inflected (known only for *Spalacotherium* and *Spalacolestes*), ?labial cingulum complete on lower molars (lacking in *Spalacotheroides*); **3**, (Spalacolestinae) meckelian groove lost; pterygoid crest extends anterodorsally to near occlusal margin of dentary, with pterygoid fossa extending well anterior to mandibular foramen (known only for *Spalacotheroides*, *Spalacolestes*); molars higher crowned, more acutely angled; upper molars with parastyle (see Patterson 1956), distal stylar cusp, and preparacrista lower than postparacrista (anterior loci); **4**, upper molars with reduced stylocone, distal stylar cusp enlarged, strong, hooklike parastyle (anterior loci), M4 strongly symmetrical, C cusp lost; M6 reduced, with paracone posteriorly placed (condition uncertain in *Spalacotheroides*, *Symmetrodontoides*), **5**, ?coronoid facet lost (condition unknown in *Spalacotheroides*, *Spalacotheridium*, *Symmetrodontoides*); upper molars with deep trigon basin, reduced parastyle (distal loci; condition unknown in *Spalacotheroides*); lower molars with paraconid and paracristid lower than metaconid and protocristid, respectively; paraconid of distal lower molars lingually placed, with paracristid distinctly longer than protocristid; upper molars with cingulum complete lingually; **6**, height differential between paraconid and metaconid on posterior lower molars pronounced; posterior lower molars broadened; m1 with taller paraconid and paracristid; M1-2 more acutely-angled, with less bulbous paracone base and more tightly arced or folded lingual face to paracone.

notably several groups of dinosaurs, appear to represent elements of a mid-Cretaceous immigration event from Asia (Cifelli *et al.* 1997). Origin of other taxa is more problematic. North American Cretaceous triconodontids, for example, appear to represent a monophyletic group, but their origin within the known Jurassic diversity of the family (both New and Old World) is uncertain (see Cifelli *et al.* 1998). If North American Spalacotheriidae are monophyletic, as we suggest, then their biogeographic ties antedate the hypothesized mid-Cretaceous interchange, as they would represent a group that was established on the continent by the Aptian-Albian, at least. Preliminary studies of somewhat older (Barremian) dinosaurs from Utah

(Kirkland *et al.* 1997) and elsewhere in North America (Norman 1998) suggest a link with the penecontemporaneous or slightly older Wealden assemblage of western Europe. *Spalacotherium*, the suggested sister-taxon to North American spalacotheriids, occurs in the Late Jurassic or earliest Cretaceous (Purbeck, see Clemens *et al.* 1979; Allen & Wimbledon 1991) to Early Cretaceous (Wealden) of England (Clemens & Lees 1971) and Spain (Krebs 1985), providing corroborative support for the suggestion of faunal continuity between North America and Europe prior to the Aptian-Albian (see, e.g., Norman 1998).

The Mussentuchit local fauna includes the most diverse assemblage of symmetrodonts known from North America, with at least four species present. There is no clear temporal trend in North American spalacotheriid diversity: one species is known from the Aptian-Albian (Patterson 1955, 1956), one from the Cenomanian (J. G. Eaton, pers. comm.), two from the Turonian (Cifelli 1990), and one each from two local faunas of the early Campanian (Fox 1976; Cifelli & Madsen 1986). In view of the tiny size of most known species, part of this may well be due to collecting biases, but it is notable that spalacotheriids are not only diverse but extremely abundant in the Mussentuchit local fauna, where they vastly outnumber all other mammals except multituberculates: evidently they were a rather successful group in the mid-Cretaceous of central Utah. Interestingly, the distribution of species is decidedly nonrandom in the upper part of the Cedar Mountain Formation. Of the thirty-two sites sampled extensively for microvertebrates, only eight (Fig. 1) yielded remains of Spalacotheriidae. The overwhelming majority of specimens referable to *Spalacolestes cretulablatta* was recovered from a single, heavily-sampled site, with fewer numbers from three other sites. *Spalacotheridium noblei*, though less abundant, is far more extensive in distribution: it is known from seven sites, and is quite rare at the major locality that produced such a wealth of specimens referable to *S. cretulablatta*. *S. inconcinnus*, on the other hand, is a rare species known from a single, poorly sampled locality – it is not present at the most heavily sampled site or, for that matter, anywhere else. Given the fact that all sites are located in a narrow stratigraphic interval and are believed to be essentially isochronous (Cifelli *et al.* 1997, 1999), we consider it unlikely that these differences are temporal in nature. All of the sites occur in fluvial overbank deposits. Although the depositional setting appears to be rather similar between sites, we attribute the distribution of Spalacotheriidae in the upper part of the Cedar Mountain Formation as being due to differences in habitat preference among species, with *Spalacolestes cretulablatta* and, particularly, *S. inconcinnus*, being characterized by a far greater degree of habitat specificity than was evidently the case for *Spalacotheridium noblei*.

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